Bull. nat. Hist. Mus. Lond. (Ent.) **69**(2):115–169 Issued 30 November 2000

Systematics of *Onirion*, a new genus of Sabethini (Diptera: Culicidae) from the Neotropical Region

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CONTENTS

SYNOPSIS. *Onirion*, a new genus of mosquitoes of tribe Sabethini from the Neotropical Region, is described and defined on the basis of shared morphological features observed in the adult, larval and pupal stages of seven species, three previously included in *Wyeomyia* Theobald and four that are new. Generic status of *Onirion* is supported by cladistic analyses of morphological data. Nominal species belonging to the genus include *Dendromyia personata* Lutz, *Goeldia luederwaldti*

Lane, *Wyeomyia* (*Dendromyia*) *belkini* Casal & García, *Wyeomyia* (*Dendromyia*) *brucei* del Ponte & Cerqueira and *Wyeomyia* (*Dendromyia*) *sirivanakarni* Duret. *Goeldia luederwaldti* is formally recognised as a junior synonym of *Dendromyia personata*. *Wyeomyia* (*Dendromyia*) *brucei* is resurrected from synonymy with *Dendromyia personata* and recognised as the senior synonym of *Wyeomyia* (*Dendromyia*) *belkini*. The taxonomic species comprising the genus are *Onirion personatum* (Lutz), *On. brucei* (del Ponte & Cerqueira), *On. celatum* sp.n., *On. sirivanakarni* (Duret), *On. imparis* sp.n., *On. regale* sp.n. and *On. aenigma* sp.n. These species are described and illustrated, and a key is provided for the identification of the adult males. The adult females, pupal and larval stages are remarkably homogeneous and for the most part no diagnostic characters are evident for their separation. The treatment of each species also includes an annotated summary of previous literature, a brief systematic discussion and information on bionomics and distribution.

Preface and acknowledgements. This manuscript was written by the first author. The second author passed away on 26 April 1999. Study of the new genus described herein was initiated by the second author in the late 1980s when we were working together at the Walter Reed Biosystematics Unit located in the Museum Support Center of the Smithsonian Institution. We were great friends, relished working together on mosquito taxonomic problems and got along famously. Because of this association, it was E.L.'s intention to name the new genus in my honour. Although I was aware of this, I was surprised to find the name *Harbachia* written in his notes and on header labels associated with the specimens that were entrusted to me several months after he died. Though I miss my good friend and colleague, I consider it a much greater honour to have had the opportunity to complete this work on his behalf than to have had the genus named after me. It is no over-statement that E.L. provided a solid foundation for the completion of this work. However, the bulk of the morphological study and all of the writing was completed by me. Hence, the responsibility for details of observation, interpretation, analysis and presentation is solely mine.

This study is based on relatively few specimens, many of which are in rather poor condition, especially some male and female genitalia that were badly damaged and over stained by whomever dissected them. Additionally, the associated larval and pupal exuviae and dissected genitalia of some specimens are missing and presumed lost. In the case of the type species, the location of reared specimens from two larval collections listed in published collection records is unknown. Despite these shortcomings, the available material is sufficient to recognise seven species, which conform to one distinct type in all life stages and form a very compact group. However, this work must be considered preliminary because too few specimens were available to determine the actual distributions and the reliability of the potentially diagnostic or differential characters in all life stages of the species. Collections consisting of adults reared from immature stages are needed from throughout Central and South America to verify many existing literature records and determine the species ranges. As new material becomes available, it seems likely that new species of the genus will also be discovered.

This work could not have been completed without the help and contributions of several people. I am most grateful to my deceased colleague and friend E.L. Peyton for beginning the study and sharing his initial findings with me. Particular thanks go to Dr Richard C. Wilkerson, Manager of the Walter Reed Biosystematics Unit (WRBU), for allowing me to resurrect and complete this study after E.L.'s death. He also provided valuable comments on the manuscript. Dr Ian J. Kitching, The Natural History Museum (NHM), assisted me with the cladistic analysis and made constructive suggestions about phylogenetic relationships. Drs Bruce A. Harrison (North Carolina Department of Natural Resources Public Health Pest Management), John F. Reinert (Center for Medical, Agricultural and Veterinary Entomology, USDA, ARS, Gainesville, Florida) and Thomas J. Zavortink (Department of Biology, University of San Francisco, California) examined the manuscript and suggested many useful improvements. I am delighted to acknowledge Ms Taina R. Litwak (formerly of WRBU) and Miss Theresa M. Howard (NHM) for preparing the superb drawings, and I am equally grateful to Mrs Joanna G. Elphick (NHM) for taking numerous photomicrographs with a computer image analysis system. The Photographic Unit of the NHM skillfully converted Joanna's images into illustrations. Joanna also assisted in finding a number of elusive literature references. Finally, I am especially grateful to Mr James E. Pecor and Mr Thomas G. Gaffigan (both of WRBU) for locating specimens, collection records and E.L.'s notes and records and sending them to me; to Prof. Oswaldo P. Forattini (Laboratório de Entomologia, Universidade de São Paulo, Brazil), Dr Diego J. Carpintero (Departmento de Entomologia Sanitaria, Instituto National de Microbiología, Buenos Aires, Argentina) and Dr Jane M. Costa (Instituto Oswaldo Cruz, Rio de Janeiro, Brazil) for the loan of specimens from their institutions.

INTRODUCTION

Despite a long history of intense study, the taxonomy of mosquitoes is far from complete and the currently accepted system of classification is not entirely natural. While the number of formally recognised species and subgenera has increased substantially since Edwards (1932) published the first catalogue of mosquitoes, the number of formally recognised genera has only increased from thirty to thirty-eight (Harbach & Sandlant, 1997; and subsequent changes to generic status by Judd, 1998; Reinert, 1999*b*, 2000*a*,*b*; Sallum *et al.*, 2000; and Navarro & Liria, 2000). As noted by Zavortink (1990), the number of recognised genera falls far short of the number expected for a family the size of Culicidae. From a comparison with groups of organisms that have reached a higher degree of beta-level taxonomy, Zavortink estimated that the total number of genera within Culicidae should be 225. Although this may never be achieved, the general trend in recent years has been to recognise more smaller generic-level taxa within the family, especially within the New World Sabethini (Zavortink, 1979; Harbach, 1991; Harbach & Peyton, 1990, 1992, 1993; Motta & Lourenço-de-Oliveira, 1995; Lourenço-de-Oliveira *et al.*, 1999).

Until relatively recently, the classification of the New World species of Sabethini was based entirely on the interpretations of Lane & Cerqueira (1942) and Lane (1953). In fact, no supraspecific changes to their classification were made until Zavortink (1979) revised the generic limits of *Trichoprosopon* Theobald, and Belkin *et al.* (1970) noted that the subgeneric classification of *Wyeomyia* Theobald appeared to be unnatural and recommended a thorough study of the immature stages to elucidate phyletic lines. Belkin *et al.* noticed the 'slit-like' development of the occipital foramen in *Wyeomyia*, as well as *Limatus* Theobald and *Sabethes* Robineau-Desvoidy, and Zavortink subsequently used this feature to distinguish larvae of *Runchomyia* Theobald (including *Isostomyia* Coquillett) from those of *Trichoprosopon*, *Shannoniana* Lane & Cerqueira and *Johnbelkinia* Zavortink. Judd (1996) later recorded the presence of dorsolateral slits in all sabethine genera except *Maorigoeldia* Edwards, *Tripteroides* Giles and the three noted by Zavortink (1979). Judd also observed the absence of slits in *Wyeomyia personata* (Lutz), one of several species recognised by Heinemann & Belkin (1977, and later publications) as members of an informal 'Subgenus B'. It became apparent that this group of species represented a new genus when one of us (E.L.P.) examined virtually every *Wyeomyia* larva and pupa in the mosquito collection of the U.S. National Museum of Natural History prior to 1990 (Harbach & Peyton, 1990). Except for these species, all other species currently included in *Wyeomyia* appear to have dorsolateral slits.

In a cladistic analysis of sabethine relationships, Judd (1996) found that *Wy. personata* appeared as a separate lineage arising between *Wy. melanocephala* Dyar & Knab and a monophyletic group comprised of species of *Limatus*, *Phoniomyia* Theobald and six subgenera of *Wyeomyia*, including the type species of *Wyeomyia*, arrayed in nine terminal clades. Further analyses utilising partitioned data supported this pattern of relationships (Judd, 1998*a*). As a result, Judd (1998*b*) formally reduced *Phoniomyia* to subgeneric status within *Wyeomyia*. *Wyeomyia melanocephala* and *Wy. personata* were both recognised as members of subgenus *Dendromyia* Theobald until Motta & Lourenço-de-Oliveira (1995) restricted the concept of this taxon to include only six species. *Wyeomyia personata* and the other nominal species previously included in *Dendromyia* were retained in *Wyeomyia* without subgeneric placement. Concordant evidence from the analyses of Judd (1996, 1998*a*) and those described below support the recognition of 'Subgenus B' as a new genus within the New World Sabethini. Because no pre-existing generic name is available for this taxon, it is formally described and given the name *Onirion* in this publication.

The new genus includes three previously described species and four new species that are described here. The former include *Dendromyia personata* Lutz, 1904*a*, *Wyeomyia* (*Dendromyia*) *brucei* del Ponte & Cerqueira, 1938 (= *Wyeomyia* (*Dendromyia*) *belkini* Casal & García, 1966) and *Wyeomyia* (*Dendromyia*) *sirivanakarni* Duret, 1982. Edwards (1932) recognised *Dendromyia* as a subgenus of *Wyeomyia* for some thirty-four species with lower mesokatepisternal setae and broad scales on the wings. Lane & Cerqueira (1942) reorganised the internal classification of *Wyeomyia* but hardly altered Edwards' concept of *Dendromyia*. They included twenty-three species that Edwards placed in the subgenus, as well as thirteen species subsequently described as species of *Dendromyia*, including seven new species that they proposed. Lane (1953), with relatively few changes, followed his earlier work with Cerqueira, and his treatment of *Dendromyia* was largely accepted until Motta & Lourenço-de-Oliveira (1995), as noted above, redefined the subgenus based largely on shared characteristics of the immature stages. In the absence of an accurate definition of *Dendromyia* prior to Motta & Lourenço-de-Oliveira, it is no wonder that the nominal species *Wy. brucei*, *Wy. belkini* and *Wy. sirivanakarni* were described as members of that taxon.

MATERIALS AND METHODS

Morphological structures were examined in the adult, pupal and fourth-instar larval stages. The majority of specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Some additional material and type specimens are deposited in The Natural History Museum, London (BMNH); Instituto Oswaldo Cruz, Rio de Janeiro (IOC); Universidade de São Paulo Faculdade de Saúde Pública, São Paulo (USP); and the Instituto Nacional de Microbiología, Buenos Aires (INM). All type specimens of new species are deposited in the USNM.

Measurements and numbers are from at least five specimens when available, and are given as a range followed by the mean or mode, respectively, in parentheses. Diagnostic and differential characters were confirmed in all specimens listed in the material examined sections. Observations of adult mosquitoes were made under simulated natural light. Larval and pupal chaetotaxy was studied using differential interference contrast microscopy. The morphological terminology follows Harbach & Knight (1980, 1982) and Harbach & Kitching (1998).

Taxonomic treatments begin with a synonymy, where applicable, and a summary of previous taxonomic treatment. The type species of each nominal taxon is given in the original combination, followed by information about the primary type specimen. References to previous taxonomic works are given in chronological order under the nomenclatural combinations used by the authors. Combinations are listed in sequence beginning with the most recent taxonomic usage. Adult females, larvae and pupae of species of *Onirion* offer little useful information for species recognition, and it is not always possible to know which species formed the basis of published records. In cases where it has not been determined which species is represented in published works, author citations are preceded by a question mark (?) in the taxonomic summaries of one or more species. Life stages are indicated by the symbols A (adult), ♂ (male), ♀ (female), L (fourth-instar larva) and P (pupa). Male and female genitalia are denoted by the letter G (genitalia) used in combination with the male and female symbols, respectively. An asterisk (*) to the right of one of these symbols indicates that at least part of the life stage or genitalia was illustrated in the publication cited. Additionally, the symbols Le (fourth-instar larval exuviae), Pe (pupal exuviae) and LU (location unknown) are used in the material examined sections.

The phylogenetic relationship of *Onirion* to other sabethine genera was examined by including character data for *Onirion* in the parsimony analysis of Harbach & Kitching (1998). Inasmuch as the procedures describing the cladistic analysis were published previously (Harbach & Kitching, 1998), they are not repeated in detail here. Briefly, forty-three genera (forty-two of Harbach & Kitching + *Onirion*) were coded for seventy-three characters (Appendix 1). Genera that were polymorphic for different states of a character were explicitly coded as possessing all those states. The data (Appendix 2) were analysed using PIWE version 2.5.1 (Goloboff, 1996). All multistate characters were treated as unordered. The commands amb-, hold 1000, hold/100, mult*50 were used in the analysis. In no instance was it necessary to further swap the cladograms found by 'mult' by using the command max*. All characters were initially equally weighted to find the most parsimonious cladograms. Implied weighting was then implemented to select among these cladograms. In the analyses, most characters were homoplastic to some degree, with observed numbers of extra steps ranging from one to more than twelve. In order to down-weight the most homoplastic characters as much as possible, implied weighting was implemented with the constant of concavity value set at $K = 1$.

ONIRION PEYTON & HARBACH, GEN.N.

TYPE SPECIES. *Dendromyia personata* Lutz, 1904a, Brazil.

Wyeomyia (subgenus B) of Heinemann & Belkin, 1977: 263, 286; Heinemann & Belkin, 1978*a*: 193, 196; Heinemann & Belkin, 1978*b*: 380, 381, 396; Heinemann & Belkin, 1979: 67, 68, 71, 83, 97, 109.

Trichoprosopon (*Isostomyia*) in part of Stone *et al.*, 1959: 75; Knight & Stone, 1977: 312.

Trichoprosopon (*Isogoeldia*) in part of Lane & Cerqueira, 1942: 506–508; Lane, 1953: 832–836.

Wyeomyia (*Dendromyia*), Series *Dendromyia* in part of Lane & Cerqueira, 1942: 537–539, 589–611; Lane, 1953: 868–879, 946–988.

Goeldia (*Isogoeldia*) in part of Lane, 1939: 165–166.

Wyeomyia (*Dendromyia*) in part of Lane, 1939: 139–148; Edwards, 1932: 86–88; Stone *et al.*, 1959: 83–88; Knight & Stone, 1977: 327–332; Gaffigan & Ward, 1985: 62.

Dendromyia (*Triamyia*) in part of Dyar, 1928: 75–77.

Wyeomyia (*Triamyia*) in part of Bonne & Bonne-Wepster, 1925: 61, 128–131.

Prosopolepis (*Triamyia*) in part of Dyar & Shannon, 1924: 481, 482.

Triamyia in part of Dyar, 1919: 116, 120.

Dendromyia in part of Theobald, 1907: 603–604; Blanchard, 1905: 634; Peryassú, 1908: 55–56, 74–75, 296–310; ?Theobald, 1910: 587–593; Surcouf & Gonzalez-Rincones, 1911: 256–263.

ADULTS. Sexes essentially identical in body size and outward appearance, exhibiting slight secondary sexual differences in antennal structure and pale scaling of mid- and hindtarsi. Medium-sized mosquitoes. Moderately ornamented; dark scaling with dull to subdued bluish iridescence when viewed from certain angles. Scales of head capsule and abdomen very broad and flat, scales of thorax moderately broad and recumbent. Vertex, occiput, most of antepronotum, scutum and scutellum dark-scaled with moderate iridescence; paratergite and mesopostnotum without scales; scaling of postgena, lower part of antepronotum, postpronotum, thoracic pleura and coxae white to silvery white. Proboscis and legs predominantly dark-scaled, proboscis darker; mid- and hindtarsi with conspicuous white scaling; wing entirely dark-scaled, without iridescence. Abdominal terga primarily dark-scaled, lateral margins pale-scaled (creamy white to light yellow), line of demarcation between dark and pale scaling essentially straight; sterna with pale scaling very nearly same colour as lateral pale patches of terga.

FEMALES. *Head*: Eyes joined above and below; interocular space constricted, without scales. Interantennal ridge absent from postfrons, with discrete frontal pit removed from postfrontal sutures. Occiput with transverse row of short, semi-erect scales at back of head. Ocular setae dark, relatively numerous, close to margin of eye; 2 long, dark, approximated interocular setae present. Scales of vertex with frosty to dirty white appearance centrally, becoming darker with stronger bluish iridescence laterally, with hint of green and yellow iridescence depending on angle of observation; few white or off-white scales at base of interocular setae; ocular line with white scales extending dorsad from postgenal scaling of same colour. Antenna dark, slightly if at all shorter than proboscis; pedicel large, surface pubescent, with minute setae and inconspicuous scales on mesal side, basal microsetae (*sensu* Harbach & Kitching, 1998) present; flagellum moderately verticillate, whorls with 10 setae, longest setae about 0.3 antenna length, flagellomere 1 with inconspicuous cluster of pale scales on mesal side. Clypeus and frons without setae and scales, with dense covering of fine silvery aculeae (pubescence). Proboscis essentially straight, slightly expanded in distal 0.3–0.4; about 0.7 length of forefemur; labellum comprised of 2 separate sclerites, proximal sclerite longer and covered in scales. Maxillary palpus short, about 0.2 length of proboscis; dark-scaled, ventral surface without scales; 2 palpomeres, proximal palpomere small, inconspicuous. *Thorax*: Integument yellowish to light brown. Dorsum with strong dark setae on anterior margin of antedorsocentral area (*sensu* Reinert, 1999*a*), supraalar area, posteriorly on either side of prescutellar area and scutellum; weaker, paler setae on mesopostnotum. Anterior promontory and mesal margin of antedorsocentral area with few broad pale scales; anterior promontory also with pale piliform scales and 2 stronger posteriorly directed setae. Antepronota moderately large, rather widely separated; scales largely same dark colour as lateral scales of vertex, small ventral area with pale scales same colour as adjacent pleural scaling. Pleura with yellow to golden setae on prespiracular, upper proepisternal, prealar, lower mesokatepisternal and upper mesepimeral areas. Lower part of proepisternum bare; upper portion of anteprocoxal membrane with scales; postprocoxal membrane with or without scales; mesopleuron with scales except on lower anterior margin of mesokatepisternum and posterior margin of mesepimeron; scales absent from mesomeron, metapleuron, metameron, postmetacoxal membrane and membrane posterior to metapleuron. Mesomeron small, dorsal margin in line with base of hindcoxa. *Wing*: Uniformly dark-scaled (brown); dorsal scales broad spatulate with rounded ends, of uniform size and shape on all veins except plume type on veins R_s, R_{2+3} and M slightly longer and those on CuA and 1A slightly smaller; no setae in basal portion of wing (dorsal or ventral). Ventral scales very similar to dorsal scales except plume type present distally on CuA and 1A; base of CuP with small scale-patch. Vein R_s without basal spur; vein R_2 much longer than vein R_{2+3}; vein 1A ends well beyond junction of mcu and CuA. Alula with piliform setae on distal half of margin. Upper calypter with 1–3 stiff setae near junction with alula; lower calypter without setae and scales. *Halter*: Scabellum without scales, integument pale; pedicel and capitellum dark-scaled. *Legs*: Coxae with white to silvery white scales. Trochanters dark-scaled dorsally, pale-scaled ventrally. Foreleg with posteroventral line of pale scaling from base of femur to apex of tarsus. Midleg with posteroventral line of white scaling on femur and tibia; tarsus with bright white scaling on anterior surface from middle of tarsomere 2 through tarsomere 5, extending onto dorsal surfaces of tarsomeres 2–4, tarsomeres 2 and 3 narrowly dark posteroventrally except at apex where pale scaling tends to encircle tarsomere, tarsomeres 3 and 4 sometimes all white. Hindleg with ventral line of white scaling on femur, tibia and proximal portion of tarsomere 1, tarsomere 2 entirely dark-scaled, distal half of tarsomere 3 through tarsomere 5 with bright white scaling ventrally, these tarsomeres narrowly dark-scaled dorsally. Forefemur about 1.5 length of proboscis, slightly longer than midfemur, about 1.25 length of hindfemur; hindtibia distinctly shorter than hindfemur, hindtarsomere 1 slightly longer than hindfemur. Ungues small, simple, black. *Abdomen*: Coloration as noted above; tergum I completely scaled except among anterolateral setae, with small posterolateral patch of pale scales concolorous and adjacent to lateral pale scaling of tergum II. Laterotergite without scales. Setae conspicuous on terga I and VIII, small and inconspicuous on posterior margins of terga II–VII; terga II–VIII with narrow lateral patches of creamy yellow scales from base to apex. Sterna II–VIII completely scaled, scales creamy yellow, scarcely if at all paler than lateral pale scaling of terga; setae pale and inconspicuous on posterior margins of sterna II–VII, darker and conspicuous on sternum VIII. *Genitalia*: Tergum VIII with rounded lateral margins, posterior border lined with several irregular rows of long setae, longest setae along posterior edge of tergum. Sternum VIII biconcave; all but anterior border and anterolateral corners covered with scales and setae; setae in more or less V-shaped patch from posterior border to middle of anterior margin. Tergum IX narrow, caudal margin straight or slightly emarginate in middle, normally with one or more setae posteriorly on either side of midline. Insula slightly longer than wide, with slight depression in middle and row of small setae on either side. Postgenital lobe as long as cerci, slightly broadened distally, caudal margin emarginate in middle; distal half of ventral surface largely covered with small setae, usually with few median setae borne on weakly sclerotized area adjacent to upper vaginal lip; distal area of dorsal surface with few slightly larger setae on either side of midline. Cercus short, flattened, covered with setae distally. 3 spermathecal capsules, one larger, each with moderate number of pores near orifice.

MALES. Like females except for sexual characters as follow. *Head*: Antenna distinctly more strongly verticillate, whorls with 14 setae, distal 2 flagellomeres not disproportionately longer than others. *Legs*: Similar to female but midleg with posteroventral line of white scaling on tarsomere 1 and tarsomeres 4 (normally) and 5 entirely dark-scaled; hindleg with continuous line of white scaling on ventral surface from base of femur to apex of tarsus. Midtarsomere 2 with white scaling encompassing distal half or less of tarsomere, sometimes all white except for narrow line of dark scaling ventrally at base; midtarsomere 3 with pale scaling on proximal portion of dorsal surface, sometimes mostly white-scaled except distally and very narrowly on ventral surface; midtarsomere 4 occasionally with few pale scales dorsoanteriorly at base. *Genitalia*: Tergum VIII (ventral in position) narrow, 3× as wide as long; posterior margin slightly concave, lined with 2–4 rows of long setae. Tergum and sternum IX fused laterally, forming a complete ring of sclerotization; tergum IX lobes not developed (except in *On. sirivanakarni*), bearing strong setae in single row or separate submedian clusters; sternum IX produced caudally between bases of gonocoxites, appearing triangular in dorsal view, apex of triangle with small sternally directed spiculate flap of weakly sclerotized cuticle (not shown in figures). Gonocoxite elongate, tapered in apical half; tergomesal surface membranous; apical sternal area covered with short setae and scales; apex on mesal side with short row of minute setae on edge of sclerotization; tergal surface with 1 or 2 groups of very long setae, proximal group a dense cluster of setae in more than one row (represented by a single seta in *On. celatum*), distal group a longitudinal row of close-set setae borne distolaterad of proximal group (absent in *On. brucei*, *On. celatum* and *On. aenigma*); tubercle of long lateral seta (*sensu* Belkin *et al.*, 1970) located a short distance distolaterad of distal tergal setae (or proximal tergal setae when distal group absent). Basal mesal lobe triangular in outline, margins irregular, largely covered with short setae, single longer seta present or absent on outer caudal angle; usually few setae on membrane immediately proximal to lobe. Gonostylus relatively simple, as long as gonocoxite, slightly curved tergally; sternal surface with small cluster of flexible piliform spicules at mid-length, bearing a flexible membranous flap in distal half (full extent of flap only apparent in illustrations of *On. brucei* and *On. celatum*); apex with 3–5 setae, usually one on sternal side and 2 shorter ones on tergal side. Aedeagus longer than wide, widest at middle; submedian tergal arms joined at midline to form a tergal bridge; apical tergal arms joined by weaker sclerotization to form an apical bridge with a small median caudal protrusion; median sternal plate moderately sclerotized, apex flared and hood-like. Proctiger strongly developed; paraproct with apex slightly enlarged, bearing small apical teeth; cercal setae numerous and very long.

PUPAE. *Cephalothorax*: Lightly pigmented with mottling of slightly darker areas on dorsum. Seta 1-CT strongly developed, long, double, usually but not always sigmoidally curved, branches with hooked apices; 8,9-CT normally single. *Trumpet*: Slightly flattened but little if at all expanded laterally; pinna short, shorter than trumpet width; meatus nearly cylindrical, slightly narrowed before pinna; supporting tubercle and tracheoid area absent. *Abdomen*: Broad central area of terga and sterna I–VII darkly pigmented; terga II–VII with distinct pair of lightly pigmented scar-like depressions (see Fig. 4A); little or no pigment around bases of some dorsal setae, especially seta 4-II–V, puncture III,IV and seta 3-IV (see Fig. 4A). Seta 1-I well developed, moderately long, dendritic, 1-II,III rather weakly developed, 1-II mesad of seta 2, 1-III laterad of seta 3, 1-IV–VII moderately developed, normally single or double; 2-II–VII near posterior margin of tergum, 2-III–VII well mesad of other dorsal setae; 3-I–III well developed, long, single, 3-II,III near caudal margin of tergum posterior to level of seta 4; 5-II,III,VII weakly developed, 5-II normally single, 5-III,VII normally multiple, 5-IV–VI strongly developed, long, usually single (sometimes forked, infrequently double or triple); 6-I–VI similarly developed, moderately long, normally single, inserted mesad and usually slightly anterior to seta 9, 6-VII weakly developed, small, normally multi-branched, inserted mesad and posterior to seta 9; 7-I slightly if at all longer than seta 6; 1-IX absent; puncture present on segments III and IV, absent from V. *Genital lobe*: Length about 0.5 mm in male, about half length of paddle in female. *Paddle*: Short, not much longer than seta 9-VIII; narrowed in distal half, spiculate at apex; asymmetrical, outer part about 1.3 width of inner part; outer margin and distal third of inner margin with minute submarginal serrations.

LARVAE. *Head*: Slightly wider than long, nearly round in dorsal view. Occipital foramen somewhat triangular with mid-ventral angle extended anterior to level of posterior tentorial pit (PTP), bounded by distinct collar.

PTP removed from collar. Hypostomal suture complete, gently curved, extending to PTP. Dorsomentum short, median tooth and most lateral (sometimes sublateral) tooth slightly longer than others. Maxilla (see Fig. 12A,B) relatively short, mesal margin produced and rounded in ventral view; maxillary brush short, composed of independent simple spicules; apical process ('apical tooth' of Harbach & Peyton, 1993) stout, rigid, tapered, slightly bent mesad, nearly half length of maxillary brush; teeth of laciniarastrum 1 in arched row, longer teeth acuminate; palpus adnate to maxillary body, triangular in ventral view with base extended mesad; maxillary sclerite apparently fused with maxillary body, seta 6-Mx borne on margin of maxillary body. Mandible (see Fig. 12C,D) short, ventrolateral margin finely spiculate. Seta 1-C strongly developed, stout; 4–7,14-C normally single, simple; 6-C midway between and well laterad of 4,5-C; 9-C in line with or slightly anterior to 10-C; 15-C small, near mid-length of labiogula, in line with 14-C. *Antenna*: Short, slender, slightly broader proximally; seta 1-A short, single, borne dorsally about 0.8 from base. *Thorax*: Integument hyaline, smooth. Seta 1,2-P long, single; 1-P removed from 2,3-P, about midway between 0-P and 2,3-P; 4-P and 7-T uniquely developed with numerous strong aciculae borne predominantly on one side of branches (see Fig. 4B and 4C, respectively); 8-M strongly developed, long, with 3–5 branches; 5-T well mesad and only slightly anterior to 6-T; 8-T ventrolaterad of plate bearing 7-T; 11-T rather stout with stiff spike-like branches in distal half; 13-T slightly longer than thorax, well developed with strongly aciculate branches, borne on small plate removed from plate supporting pleural setal group. *Abdomen*: Integument hyaline, smooth. Seta 1-I,II moderately developed, mesad of seta 2, 1-III–VII strongly developed, especially on segments III–V, 1-III,IV laterad of seta 4, 1-V–VII laterad of seta 2; 2-I,II anterolaterad of seta 1, 2-III–VII well mesad of other dorsal setae; 3-I,II moderately long, slightly longer than seta 1, 3-III–VI strongly developed, about length of seta 1, 3-VII very long, reaching apex of siphon; seta 5-I,II weakly developed, 5-III–VI strongly developed, similar to setae 1 and 3; 6-I–VI strongly developed, 6-I,II multi-branched, 6-III–VI single; seta 13-I,II small, borne well mesad of other ventral setae, 13-III–V very long, single, 13-III mesad of other ventral setae but well laterad of 13-I,II, 13-IV,V displaced laterad of setae 11 and 12; puncture present on segments III and IV, absent from V. *Segment VIII*: Comb plate absent; scales largest dorsally, becoming progressively smaller and more lightly pigmented ventrally, in irregular single row; individual scales relatively narrow, tapered, evenly fringed. Seta 1-VIII immediately dorsad of most dorsal comb scale; 2–5-VIII posterior to dorsal half of comb; 1,3-VIII similarly developed, small, multi-branched; 2,4,5-VIII moderately developed, fairly long, single. *Siphon*: Widest at base and gradually narrowed to apex; lightly pigmented with basal edge darkly pigmented; surface smooth except for some minute inconspicuous rows of spicules basally. Filamentous pecten extends from base to near apex of siphon; basal filaments in 2 rather irregular close-set rows that gradually merge to form a single row beyond level of seta 1-S. Seta 1-S moderately developed, single, arising a distance above base of siphon equal to approximately one-third of siphon length; 1a,2a-S each represented by 2 setae near apex of siphon; 1a-S longer than diameter of siphon at point of attachment, usually single; 2a-S small, multi-branched; 2-S strong, laterally compressed, comb-like, with row of short denticles on one side beyond basal third. *Segment X*: Saddle relatively large, extending below lateral midline of segment. Setae 1–3-X well developed, very long, single; seta 4-X well developed, multi-branched, about half length of seta 1, without basal support plate.

EGGS. Unknown.

ETYMOLOGY. *Onirion* is derived from the Greek *Oneiros* (m.), dream or vision. Addition of the diminutive suffix *–ion* results in a neuter name meaning 'little dream'. It should be pronounced *Oh-near-ee-un* (*O* as the 'o' in <u>o</u>pen, *nir* as the 'neer' in s<u>*neer*</u>, *i* as the 'i' in mach<u>i</u>ne and *on* as the 'on' in t<u>*on*</u>). In keeping with the practice initiated by Reinert (1975), the two-letter abbreviation *On.* is recommended for this genus.

DISCUSSION. *Onirion* differs markedly from other genera of Sabethini. The larvae are easily distinguished by the predominance of aciculae on one side of the branches of setae 4-P and 7-T, the stout apically spiked seta 11-T, the placement of strongly developed seta 13-IV,V laterad of setae 11 and 12, and the presence of a dense filamentous pecten extending the length of the siphon. Pupae have punctures only on terga III and IV, a noticeable pair of scar-like depressions borne centrally on terga II–VII and terga I–VII are largely darkly pigmented centrally with little or no pigment around the bases of many setae. Adults are similar to *Wyeomyia* in overall ornamentation, but the pale markings on the tarsi are quite characteristic of *Onirion*. In the male genitalia, the development of cercal setae is greater than in any other genus and is distinctive of *Onirion*. The collection of long tergal setae on the gonocoxites (except *On. celatum*) is an unusual feature but is closely approximated in a number of other sabethine taxa, e.g. subgenus *Exallomyia* Harbach & Peyton of *Wyeomyia*.

Onirion consists of a small, homogeneous assemblage of species whose relationships cannot be determined at present because of the paucity of anatomical distinctions available for a meaningful cladistic analysis. The species are differentiated in adult males, but are only weakly if at all differentiated in the adult females and immature stages. *Onirion* *brucei* (as *Wy. belkini*) and *On. sirivanakarni*, as well as the four new species described below, would not have been recognised as species distinct from *On. personatum* if the males of these species had remained unknown. Because the females, larvae and pupae are virtually identical, accurate identification may require the elucidation of species-specific DNA sequences. However, the close similarity of the species in all life stages would seem to indicate little overall genetic divergence between them.

Species of *Onirion* can be divided into two groups based on the presence or absence of distal tergal setae on the goxocoxites of males. This character appears to be indicative of natural affinities. The Personatum Group includes *On. personatum*, *On. sirivanakarni*, *On. imparis* and *On. regale*. These species possess both proximal and distal tergal setal groups. The genitalia of *On. sirivanakarni* and *On. regale* exhibit autapomorphic characters that suggest these species may have diverged from an ancestral form similar to the other two species. The Brucei Group includes *On. brucei*, *On. celatum* and *On. aenigma*. Distal tergal setae are absent in these species. *Onirion celatum* differs from the others in having only one proximal tergal seta, which appears to be the derived state within the group. It is impossible to know at this time whether the presence of one or two groups of tergal setae is the plesiomorphic condition.

BIONOMICS. Little reliable bionomical information is available for species of *Onirion*. All species are sylvan, and adults are active during the daytime. Females are attracted to humans, but the species are of no known medical importance. The immature stages are only definitely known to inhabit bamboo internodes (one specimen of *On. sirivanakarni* from a terrestrial bromeliad requires confirmation). Records of immatures collected in other phytotelmata and artificial containers probably refer to species of other genera.

DISTRIBUTION. Species of *Onirion* are only definitely recorded from Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Brazil, Bolivia and Argentina. Species of the genus probably occur in tropical forests from southern Mexico to northern Argentina.

PHYLOGENETIC RELATIONSHIPS

In the cladistic analyses, most characters were homoplastic to some degree, with observed numbers of extra steps ranging from one to more than twelve. In order to down-weight the extremely homoplastic characters as much as possible within the limits of PIWE, a constant of concavity (*K*) value of 1 was applied. Two most parsimonious cladograms (MPCs) were then obtained with fit = 285.8 and a length of 311 steps (CI = 0.31, RI = 0.68). Since the topology of the Culicini + Sabethini clade was the same in these MPCs, this portion of the strict consensus of the two cladograms is illustrated in Fig. 1B. Character changes for the numbered nodes are listed in Appendix 3. The topology of the Culicini + Sabethini clade obtained by Harbach & Kitching (1998) in the absence of *Onirion* is included in Fig. 1A for comparison.

Prior to the recent reduction of *Phoniomyia* to subgeneric status within *Wyeomyia* (Judd, 1998*b*), nine sabethine genera were recognised in the New World: *Isostomyia, Johnbelkinia, Runchomyia, Shannoniana, Trichoprosopon, Phoniomyia, Limatus, Sabethes* and *Wyeomyia*. Based on historical associations (Judd, 1996) and the pattern of relationships shown in Fig. 1A, these genera can be divided into two functional groups: the *Trichoprosopon* group, which includes the first five genera, and the *Sabethes* group, which includes the last four genera. When *Onirion* is included in the analysis, this arrangement of taxa is disrupted between nodes 65 and 61. The trichotomy at node 65 is resolved in favour of placing *Trichoprosopon* as the sister group to *Johnbelkinia* + *Runchomyia* (node 60 in Fig. 1B), and *Onirion* is placed in an unresolved relationship with *Isostomyia* + *Shannoniana* and the *Sabethes* group (node 66 in Fig. 1B). The sister-group relationship of *Trichoprosopon* + (*Johnbelkinia* + *Runchomyia*) is supported by an interesting feature of the wing: vein R_s with a basal spur (ch. 64: 0 → 1, with independent occurrence at node 62). Although this clade is supported by only one synapomorphy, there is little homoplasy in the distribution of the applicable character states; thus, the character appears to provide fairly strong support for the relationship. Node 66 is also supported by a single synapomorphy: postpronotal setae absent (ch. 55: 1 → 0). Since this condition occurs elsewhere only in *Anopheles* Meigen, *Bironella* Theobald (not recognized as genus by Sallum *et al.*, 2000) and *Toxorhynchites* Theobald, it appears to be an important character providing strong support for the terminal clade.

Within the trichotomy defined by node 66, the sister-group relationship of *Isostomyia* + *Shannoniana* (node 58) is only supported by a feature of the larval mouthparts: maxillary brush represented by a solid claw-like structure (ch. 8: 0 → 2). This character only occurs elsewhere in subgenus *Rachisoura* Theobald of *Tripteroides*. The monophyly of the *Sabethes* group (node 63) is supported by three synapomorphies: slit-like occipital foramen (ch. 2: 0 → 1, with occurrences at node 64 and in *Runchomyia* and *Isostomyia*), apical flagellomeres of males not disproportionately long (ch. 42: 0 → 1, homoplastic) and upper calypter without setae (ch. 62: 1 → 0, with six independent occurrences in Culicidae, one in Sabethini at node 64). Whether the inclusion of additional character data in the analysis would resolve the trichotomy is a moot question.

Despite the results of the cladistic analyses reported here and by Judd (1996), the affinities of *Onirion* are ambiguous. The larvae resemble *Trichoprosopon*, *Shannoniana* and *Johnbelkinia* in having a circular occipital foramen, but resemble *Isostomyia*, *Runchomyia* and many phyletic lines of the *Sabethes* group in the presence of a filamentous pecten on the siphon. The latter taxa, however, have a slit-like occipital foramen. The larvae of *Onirion* have unique features that distinguish them from all other New World sabethine genera, including the concentration of aciculae on one side of the branches of setae 4-P and 7-T, the stout seta 11-T with multiple apical spikes and the strong development and placement of seta 13-IV,V lateral to setae 11 and 12. The pupae of *Onirion* have punctures on abdominal segments III and IV. Punctures are absent in *Trichoprosopon* and *Shannoniana*, present on segments IV and V in *Johnbelkinia*, present on segments III–V in *Isostomyia* and *Runchomyia*, and occur in various combinations from all present to all absent in members of the *Sabethes* group. The male genitalia of *Onirion* are unusual in the radical development of the cercal setae and the tergal setae of the gonocoxite, but the basal mesal lobe is detached from segment IX and borne on the tergomesal surface of the gonocoxite as it is in most members of the *Sabethes* group (note that Judd, 1996, incorrectly scored the basal mesal lobe as absent in *Wy. personata*). All genera of the *Trichoprosopon* group have the basal mesal lobe fused to segment IX and distinctly separated from the gonocoxite. The maxillary palpus of *Onirion* males is composed of two palpomeres, a condition shared with *Isostomyia*, *Runchomyia* and the *Sabethes* group. Males of *Trichoprosopon*, *Johnbelkinia* and *Shannoniana* have maxillary palpi composed of five palpomeres.

Without a thorough review of Sabethini at species level, it is difficult to determine the affinities of *Onirion*. From an intuitive interpretation of available anatomical data, the genus probably represents a specialized offshoot from the ancestral stock that gave rise to *Isostomyia*, *Runchomyia* and the *Sabethes* group.

IDENTIFICATION OF SPECIES

Except for adult males, species of *Onirion* are remarkably homogeneous in all life stages. Because discrete anatomical differences are not evident for distinguishing adult females, larvae and pupae, only a key to males is provided below. Characters that may partially or potentially differentiate females, larvae and pupae are recounted following the key.

Key to males of *Onirion*

1. Ventral surface of proboscis partly white-scaled with bright blue iridescence when viewed from certain angles; tergum IX with short flattened setae in more or less continuous row 2

– Ventral surface of proboscis partly or completely yellow-scaled; tergum IX with short setae distinctly separated into lateral groups, or with long setae in more or less continuous row 3

2. Proximal half of proboscis with semi-erect scales imparting a shaggy appearance, ventral white scaling in 4 more or less distinct patches, one distal and 3 median (Fig. 2D,E); gonocoxite with a single proximal tergal seta (no distal tergal setae) (Fig. 15A) .... *celatum*

– Proboscis without shaggy appearance proximally, ventral white scaling confined to distal end of prementum (Fig. 2B,C); gonocoxite with a cluster of proximal tergal setae (no distal tergal setae) (Fig. 9G) .... *brucei*

3. Proboscis enlarged beyond middle, enlarged portion with ventral patch of bright yellow scales and lateral tufts of long black scales 0.75 from base, distal 0.25 narrower and often abruptly upturned (Fig. 3A,B); tergum IX with widely separated lobes, each bearing numerous short setae and one large seta (Fig. 15J) .... *sirivanakarni*

– Proboscis slightly expanded distally but not noticeably enlarged beyond middle, most or all of ventral surface yellow-scaled, brighter yellow distally; tergum IX without lobes, setae otherwise 4

4. Postprocoxal scales usually absent; gonocoxite with both proximal and distal tergal setal groups, these contiguous 5

– Postprocoxal scales usually present; gonocoxite with only proximal tergal setal group or both groups present but widely separated 6

5. Ventral surface of proboscis always entirely yellow-scaled, with yellow scaling extended onto lateral and dorsal surfaces at base (Fig. 2A); tergum IX with short flattened setae separated into lateral groups (Fig. 9D) .... *personatum*

– Ventral surface of proboscis not always yellow-scaled in proximal half, yellow scaling not extending onto lateral and dorsal surfaces basally (Fig. 3D); tergum IX with rather long slender setae in more or less continuous row (Fig. 18J) .... *regale*

6. Gonocoxite with both proximal and distal tergal setal groups, these widely separated (Fig. 18A); tergum IX with rather long flattened setae in more or less continuous row (Fig. 18D) .... *imparis*

– Gonocoxite with cluster of proximal tergal setae, distal tergal setal group absent (Fig. 9G); tergum IX with short flattened setae narrowly separated into lateral groups (somewhat intermediate between *personatum*, Fig. 9D, and *brucei*, Fig. 9J) .... *aenigma*

Females

Females of *On. sirivanakarni* are distinguished by the unusual development of tergum IX, which is produced posteriorly on either side of the midline, with each lobe bearing a cluster of setae (Fig. 13H). The entirely dark proboscis of *On. brucei*, *On. celatum*, *On. imparis* and *On. regale* distinguish these species from the others. The available specimens of *On. regale* do not have scales on the postprocoxal membrane, but this character, even if it holds true, will not distinguish females of this species from the others that have an entirely dark proboscis because the scales are not always present in those species. *Onirion personatum* and *On. aenigma* have a ventral streak of pale scaling on the distal half of the proboscis. Since *On. personatum* occurs in eastern Brazil and *On. aenigma* is probably confined to the foothills and plains on the east side of the Andes Mountains of Peru and Bolivia, individuals of these two species can be identified on the basis of provenance.

Pupae

The pupal stages of *On. sirivanakarni* and *On. regale* are unknown. The trumpet is generally larger in *On. celatum* (see species descriptions). Setae 1-CT is rather variable in *On. brucei* but tends to be weakly if at all sigmoidal. Seta 10-CT is usually single (sometimes forked apically) in *On. personatum*, *On. brucei* and *On. imparis*, whereas it is usually double (sometimes triple) with the branches arising basally in *On. celatum* and *On. aenigma*. Seta 1-II usually has more branches in *On. celatum* than the other species. Seta 6-VII is larger, noticeably longer than seta 5-VII, and usually has fewer branches in *On. brucei* and *On. aenigma*. This seta is never longer than seta 5 in the other species. Finally, *On. personatum* has the longest paddle: equal to or greater than 0.68 mm in this species and less than 0.68 mm in the other species. These observations are based on few specimens, and the perceived taxonomic value of the characters may diminish once the full range of variation is known for the individual species.

Larvae

The larva of *On. sirivanakarni* is unknown. The sclerotized parts (head, antenna, siphon and saddle) of *On. personatum* are generally larger than in the other species. Based on available specimens, only *On. regale* exhibit any overlap in the size of the head with *On. personatum* (see species descriptions). Seta 5-III–VI is double in these two species and normally single in the others. Seta 1-IV,V is single in *On. aenigma* and double in the other species. *Onirion celatum* tends to have a greater number of comb scales and *On. aenigma* tends to have fewer. On the average, *On. brucei* has a larger siphon index. Finally, the ventral anal papillae are longer in *On. brucei* and *On. aenigma*, about 4.5 times longer than the saddle. These structures are slightly less than 3 times the length of the saddle in *On. personatum* and only about 1.5 times longer than the siphon in *On. celatum* and *On. imparis*. Too few specimens were available for study to know to what degree, if any, the size of the anal papillae is influenced by the aquatic milieu where the larvae live.

SPECIES TREATMENTS

Onirion personatum (Lutz)

(Figs 2, 5–9)

1904. *Dendromyia personata* Lutz, 1904*a*: 22–26; 1904b: 68 (♀ ♂). Lectotype ♂, Cantareira [São Paulo], Brazil (BMNH); designation by Belkin *et al.*, 1971: 11; examined. Bruijning, 1959: 112 (synonymy with *aporonoma* Dyar & Knab). **Comb.n.**

1936. *Goeldia* (*Isogoeldia*) *luederwaldti* Lane, 1936*a*: 6–7. Holotype ♀, Fazenda José Euphrasio, Avaré, [São Paulo], Brazil (USP); examined. **Syn.n.**

Wyeomyia personata of Peryassú, 1923: 87 (Brazil; list); Deane *et al.*, 1953: 103, 106 (Brazil; A bionomics); Forattini, 1965: 159, 160, 162 (Brazil; A L bionomics); Cova Garcia *et al.*, 1966: in part, ♂, 74, 353 (Vol. I) and 313 (Vol. II), taken from Lane, 1953; Forattini *et al.*, 1970: 89 (in part, Brazil records from Rio de Janeiro and São Paulo only, specimen data; Panama record = *Wyeomyia* sp.); Forattini *et al.*, 1988: 546 (Brazil; specimen data); Motta & Lourenço-de-Oliveira, 1995 (removal from subgenus *Dendromyia*); Guimarães, 1997: in part, 130–131 (Brazil only; info. on type; literature; synonymy); Judd, 1998*a*: 68–71, 73, 76–79, 81, 83, 86, 89, 90, 93 (phylogenetic relationships); Guimarães *et al.*, 2000*b*: 20 (Brazil; A bionomics).

Wyeomyia (*Dendromyia*) *personata* of Edwards, 1932: 88 (Brazil; list); Lane, 1939: 146 (in part, Brazil records only, literature; Venezuela record = *On. imparis*); da Costa Lima, 1943: 305–306 (Brazil; A; taxonomy); Lane, 1953: 869, 870, 874, 876, 962–964 (Brazil, excluding records from Mato Grosso and Venezuela; A ♂G P L keys; ♀ ♂* P* L*; distribution); Horsfall, 1955: 329 (Brazil only); Stone *et al.*, 1959: 86–87 in part (Brazil only; info. on type; literature; synonymy); Cerqueira, 1961: 159–160 (Brazil, records from Amazonas and Amapá questionable; collection record; A L bionomics); Belkin, 1968: 41 (Brazil; info. on type);

Belkin *et al.*, 1971: 11 (info. on type; L bionomics); Neves & Pedersoli, 1976: 552 (Brazil; list); Knight & Stone, 1977: 330 in part (Brazil only; info. on type; literature, synonymy); Guimarães & Arlé, 1984: 313, 314, 316, 317, 320 (Brazil; A bionomics); Guimarães *et al.*, 1985: 174, 176, 177, 179, 180 (Brazil; A bionomics); Guimarães & Victório, 1986: 95, 96, 98, 101 (Brazil; A bionomics); Guimarães *et al.*, 1987: 278–280, 282–285 (Brazil; A bionomics); Guimarães *et al.*, 1989: 248–252 (Brazil; A bionomics); Sant'Anna de Souza *et al.*, 1994: 185 (Brazil; list); Judd, 1996: 137, 138, 141, 148, 150 (phylogenetic relationships); Guimarães *et al.*, 2000*a*: 6, 8 (Brazil; A bionomics).

Wyeomyia (subgenus B) *personata* of Heinemann & Belkin, 1979: 67, 68, 71, 83 (Brazil; collection record; L bionomics).

Dendromyia (*Triamyia*) *personata* in part of Dyar, 1928: 68, 76–77 (excluding ♀ = ?*Wy. aporonoma*) (Brazil; A key; ♂).

Wyeomyia (*Triamyia*) *personata* of Bonne & Bonne-Wepster, 1925: 60, 131 (Brazil; A key; ♀).

Prosopolepis (*Triamyia*) *personata* [*sic*] of Dyar & Shannon, 1924: 482.

Triamyia personata of Dyar, 1919: 120 (A key); Bonne-Wepster & Bonne, 1921: 11–12 (♂).

Dendromyia personata of Blanchard, 1905: 634 (Brazil; list); Theobald, 1907: 603, 604 in part, excluding ♂G of Pl. IX (Brazil; A key); Peryassú, 1908: 55, 74–75, 297–298, ?Fig. 54 (Brazil; A key; ♀ ♂ L*; ?collection record); ?Theobald, 1910: 587, 592 (Brazil; A key; L*); Surcouf & Gonzalez-Rincones, 1911: 259 (Brazil: ♀); del Ponte, 1939: 541 (Brazil; A); Townsend, 1990: 120 (Brazil; info. on type).

Wyeomyia (*Dendromyia*) *brucei* of Lane, 1939: 140 (Brazil; catalogue); Lane & Cerqueira, 1942: 538, 539, 544, 546, 598–599, 738–739 (Figs 156–159), 793 (Fig. 340), 824–825 (Figs 410, 411) (Brazil; A ♂G P L keys; ♀ ♂* P* L*; L bionomics; distribution); Horsfall, 1955: 328 (Brazil; L bionomics); Belkin *et al.*, 1971: 11 (info. on type; L bionomics).

Wyeomyia brucei of Davis, 1944: 229 (Brazil; collection record; L bionomics); Davis, 1945: 255 (Brazil; collection record; A bionomics).

Dendromyia brucei of del Ponte, 1939: 540 (Brazil; A).

Wyeomyia luederwaldti of Zavortink, 1979 (transfer from genus *Trichoprosopon*); Guimarães, 1997: 129 (Brazil; info. on type).

Trichoprosopon luederwaldti Forattini *et al.*, 1970: 79–80 (Brazil; info. on type).

Trichoprosopon (*Isostomyia*) *luederwaldti* of Stone *et al.*, 1959: 75 (Brazil; info. on type); Belkin *et al.*, 1971: 9 (info. on type); Knight & Stone, 1977: 312 (Brazil; info. on type).

Trichoprosopon (*Isogoeldia*) *luederwaldti* of Lane & Cerqueira, 1942: 508 (Brazil; ♀); Lane, 1953: 816, 835–836 (Brazil; ♀).

Goeldia (*Isogoeldia*) *luederwaldti* of Lane, 1939: 165 (Brazil; literature).

Goeldia Luederwaldti [*sic*] of Lane, 1937: 125 (Brazil; collection record).

ADULT. As described for genus. Measurements in Table 1; numbers of setae in Table 2. *Thorax*: Postprocoxal scales more often absent than present. Pleural scaling generally silvery white.

FEMALE (Figs 5, 6). Proboscis dark-scaled with streak of pale scales on distal half of ventral surface, streak widest before labella, sometimes rather indistinct. *Genitalia* (Fig. 7C-H): As illustrated; tergum IX with 1 or 2 setae on either side of midline; insula with 8 setae on either side; dorsal surface of postgenital lobe with 4–6 setae distally on either side of midline.

MALE. Ventral surface of proboscis (Fig. 2A) broadly yellow-scaled from base to apex of prementum; pale scaling extended laterally and dorsally at base; bright yellow in distal half, duller in proximal half. Maxillary palpus same dull yellow colour as base of proboscis. *Genitalia* (Fig. 9A-F): Tergum IX without lobes, bearing 2–4(4) strong flattened setae on either side of narrow median bridge, apices of setae bent slightly laterad. Gonocoxite with proximal and distal tergal setal groups; proximal group a tight cluster of 35–54 ($\bar{x}$ = 44) long slender flexible setae (about 0.7 length of gonocoxite), contiguous with distal group; distal group a longitudinal row of 17–26 ($\bar{x}$ = 20) longer and thicker close-set setae (slightly longer than gonocoxite). Basal mesal lobe with single long seta on caudal angle. Proctiger with 18–25(20) cercal setae.

PUPA (Fig. 7). As described for genus; character and positions of setae as figured, numbers of branches in Table 3. *Cephalothorax*: Seta 1-CT normally strongly sigmoid; 10-CT usually single, sometimes forked apically. *Trumpet*: Length 0.33–0.41 mm ($\bar{x}$ = 0.37 mm), pinna 0.04–0.09 mm ($\bar{x}$ = 0.07 mm), width at mid-length 0.12–0.15 mm ($\bar{x}$ = 0.13 mm), index 2.43–3.17 ($\bar{x}$ = 2.74). *Abdomen*: Length 3.9–4.4 mm ($\bar{x}$ = 4.1 mm). Seta 1-II usually double (1–3); 6-VII no longer than 5-VII, with 2–8(5) branches. *Genital lobe*: Length about 0.35 mm in female, about 0.50 mm in male. *Paddle*: Length 0.68–0.80 mm ($\bar{x}$ = 0.73 mm), width at widest point 0.44–0.53 mm ($\bar{x}$ = 0.48 mm), index 1.37–1.63 ($\bar{x}$ = 1.51).

LARVA (Fig. 8). As described for genus; character and placement of setae as figured, numbers of branches in Table 4. Generally larger than other species. *Head*: Length 1.18–1.37 mm ($\bar{x}$ = 1.30 mm); width 1.28–1.52 mm ($\bar{x}$ = 1.37 mm). Dorsomentum with 10–12(11) teeth on either side of median tooth. Maxilla with 11–16(13) lateral teeth (laciniarastrum 1). *Antenna*: Length 0.32–0.35 mm ($\bar{x}$ = 0.34 mm). *Abdomen*: Setae 1-IV,V and 5-III–VI double. *Segment VIII*: Comb with 15–

18(17) scales. *Siphon*: Length 1.40–1.70 mm (x̄ = 1.50 mm), width at base 0.29–0.42 mm (x̄ = 0.36 mm), index 3.57–4.84 (x̄ = 4.25); pecten with 99–132 filaments (x̄ = 115). *Segment X*: Saddle length 0.32–0.39 mm (x̄ = 0.36 mm); siphon/saddle index 3.89–4.69 (x̄ = 4.21). Dorsal anal papillae about length of saddle, ventral anal papillae about 2× length of saddle.

DISCUSSION. Lane & Cerqueira (1942) confused the descriptions and illustrations of *On. personatum* (as *Wy. personata*) and *On. brucei* (as *Wy. brucei*), which they recognised as separate species. They also synonymised *Wy. aporonoma* Dyar & Knab with *Wy. personata*. The interesting aspect is that the male genitalia, larva and pupa that Lane & Cerqueira described and illustrated for *Wy. personata* actually apply to *Wy. aporonoma*, and those of *Wy. brucei* apply to *Wy. personata*. Most of the larval habitats listed for *Wy. personata* are those utilised by *Wy. aporonoma*. This problem was corrected in Lane (1953) when he recognised *Wy. aporonoma* as a valid species. Unfortunately, Lane mistakenly synonymised *Wy. brucei* with *Wy. personata*, undoubtedly based on the male genitalia of *Wy. personata* collected in Rio de Janeiro that were incorrectly identified as *Wy. brucei*. There are seven specimens from Rio de Janeiro State in the USNM and BMNH collections that are labelled as paratype males of *Wy. brucei*, and these probably contributed to Lane's decision to place *Wy. brucei* in synonymy with *Wy. personata*. These specimens were collected in the same year that del Ponte & Cerqueira (1938) described *Wy. brucei* from eleven females captured in Cuiabá (as Cuyabá), Mato Grosso in 1935; hence, they are invalid paratypes of this nominal species. As indicated below, *On. personatum* appears to be confined to eastern Brazil where *On. brucei* is not known to occur. At present, there is no evidence that *On. personatum* occurs in sympatry with any other species of the genus.

Zavortink (1979) examined a female of *Goeldia* (*Isogoeldia*) *luederwaldti* Lane, presumably the holotype, from the Universidade de São Paulo and noted that it was 'similar to, and perhaps even the same as, *Wyeomyia* (*Dendromyia*) *personata* (Lutz 1904)'. This observation led Zavortink to transfer *luederwaldti* from *Trichoprosopon*, where it was placed by Lane & Cerqueira (1942), to *Wyeomyia*. The holotype female is in relatively good condition and easily identified as a species of *Onirion*. Based on provenance, it can only be *On. personatum*.

Onirion personatum appears to be most closely related to *On. regale*. The males of these two species are very similar, exhibiting ostensible differences only in the degree of pale scaling on the proboscis and the development of setae on tergum IX of the genitalia.

BIONOMICS. Females of *On. personatum* are readily attracted to humans in forest during the day (Cerqueira, 1961; Guimarães & Arlé, 1984). Davis (1945) captured this species (as *Wy. brucei*) on avian and human bait. In a study using human, opossum and chicken baits, Guimarães *et al.* (1987) found that 65% of captured females were attracted to humans, 11% to opossum and 24% to chicken. Using human bait, Deane *et al.* (1953) and Guimarães *et al.* (1985) collected significantly more specimens at ground level than in forest canopy. Guimarães & Victório (1986) found this species to be most abundant at human bait during the morning hours, with peak activity between 10.00 and 12.00 hours. They also captured a few females attempting to bite in late afternoon. In recent studies by Guimarães *et al.* (2000*a*,*b*), females attracted to humans were captured between November and March mainly in forest but also in an area of shrub (*sic*, = scrub?) vegetation. The immature stages of this species are only definitely known to inhabit bamboo. Larvae have been collected from cut bamboo and living and dead internodes with man-made openings (cuts) and beetle holes (Cerqueira, 1961; Davis, 1944; Heinemann & Belkin, 1979). Immature stages collected in Brazil were found in association with *Corethrella appendiculata* Grabham, *Culex* (*Carrollia*) *soperi* Antunes & Lane, a member of the *Cx.* (*Microculex*) *imitator* subgroup, *Cx.* (*Mcx.*) *neglectus* Lutz, *Orthopodomyia albicosta* (Lutz), *Sabethes* (*Peytonulus*) *aurescens* (Lutz), *Shannoniana fluviatilis* (Theobald), *Trichoprosopon digitatum* (Rondani), *Tr. pallidiventer* (Lutz), a species of *Toxorhynchites* (*Lynchiella*), *Wyeomyia* (*Wyeomyia*) *limai* Lane & Cerqueira and *Wy.* (*Wyo.*) ?*oblita* (Lutz). Reports of larvae taken from ground bromeliads and old cans (Peryassú, 1908; Davis, 1944) probably refer to species of *Wyeomyia*.

DISTRIBUTION. *Onirion personatum* is only definitely known to occur in eastern Brazil (Fig. 20C), where it appears to be associated with the Atlantic rain forest system. Records from Bolivia (Cerqueira, 1943; Prosen *et al.*, 1963) probably refer to either *On. aenigma*, *On. brucei*, *On. celatum* or any combination of these species. Four females from western areas of Mato Grosso, Brazil (Lane & Cerqueira, 1942; Lane, 1953) examined during this study appear to be *On. brucei*. Records of this species from localities in the states of Amazonas and Amapá, Brazil (Cerqueira, 1961) require confirmation. Published reports of *On. personatum* in Argentina, Colombia, Mexico, Panama and Venezuela almost certainly apply to other species.

MATERIAL EXAMINED.
Ninety-four specimens (19♀, 34♂, 14♀G, 1♂G, 12Le, 14Pe), including fourteen individual rearings. *Lectotype* ♂ of *Dendromyia personata*, with dissected genitalia on microscope slide, BRAZIL: *São Paulo*, Cantareira; *paralectotype* ♂, with head, wings and legs on 3 separate microscope slides and dissected genitalia on acetate strip on pin (remainder of specimen lost) (BMNH). *Holotype* ♀ of *Goeldia luederwaldti* (439), BRAZIL:

São Paulo, Avaré (USP). *Non-types*, BRAZIL: 8♀ 15♂ 5♂G, *Rio de Janeiro*, Cachaeira, Faz. Martinez, May 1938 (1♂ 1♂G, invalid paratype of *Wy. brucei*) (USNM); Mangaratiba, May 1938 (1♂ 1♂G, invalid paratype of *Wy. brucei*), Junho 1938 (1♂), Julho 1938 (1♀) (USNM), Junho 1938 (1♂, invalid paratype of *Wy. brucei*) (BMNH); Petrópolis, April 1938 (3♀), May 1938 (3♀ 3♂) (USNM), May 1938 (1♂ 1♂G, invalid paratype of *Wy. brucei*) (BMNH); Terezópolis, April 1938 (1♀ 2♂), May 1938 (4♂ 2♂G, including 2 invalid paratypes of *Wy. brucei*) (USNM), May 1938 (1♂, invalid paratype of *Wy. brucei*) (BMNH). 1♀, *Pará*, Belém, 23.8.53 (*Duret*) (USNM); 1♀ 3♂ 3♂G 4Le 4Pe, *Paraná*, Quartas Barras, Estr. da Graciosa, Serra do Mar, 7.X.1979 (1LePe♂ 1♂G – E-6264), 10.11.1981 (1LePe♀ – E-6261), 10.IV.1981 (2LePe♂ 2♂G – E-6262, E-6263) (*A. Lozovei*) (USP); 2♀ 6♂ 2♂G 8Le 10Pe, *São Paulo*, Juguiá, Jan 1943 (1LePe♀ – 3869; 1LePe♂ – 3868); Taubaté, Maristela Farm, bambu fechado. mata, 17.x.1989 (1LePe♀ 5LePe♂ 2Pe♂ 2♂G) (*Gomes*) (USP).

Onirion brucei (del Ponte & Cerqueira)

(Figs 2, 4, 9–12)

1938. *Wyeomyia* (*Dendromyia*) *brucei* del Ponte & Cerqueira, 1938: 231–232 (♀). Holotype ♀, Cuyabá [Cuiabá], Mato Grosso, Brazil (IOC, Marchon-Silva *et al*., 1996: 476); examined. Synonymy with *Dendromyia personata* Lutz by da Costa Lima, 1943: 306. **Comb.n. & Stat.n.**

1966. *Wyeomyia* (*Dendromyia*) *belkini* Casal & García, 1966: 155–161 (♀*♂* P* L*). Holotype ♂, Misiones (Igu 26), Argentina (INM); examined. **Syn.n.**

Wyeomyia (*Dendromyia*) *belkini* of Barrera Oro *et al*., 1966 (Argentina; collection record); Belkin *et al*., 1968: 11 (info. on type; A L bionomics); Knight & Stone, 1977: 328 (Argentina; info. on type); Louton *et al*., 1996: 232, 234 (Peru; L bionomics).

Wyeomyia belkini of Guimarães, 1997: 128 (Argentina; info. on type).

Wyeomyia personata in part of Forattini *et al*., 1970: 89 (Brazil records from Mato Grosso only, specimen data); Guimarães, 1997: 130 (Argentina, ?Bolivia).

Wyeomyia (*Dendromyia*) *personata* of Duret, 1950*a*: 228, 232 (Argentina; collection record); Duret, 1951: 376 (Argentina; collection record); Stone *et al*., 1959: 86–87 in part (Argentina, ?Bolivia); Castro *et al*., 1960: 560 (Argentina; collection record); ?Prosen *et al*., 1963: 79, 80 (Bolivia; collection record; A bionomics); Knight & Stone, 1977: 330 in part (Argentina, ?Bolivia).

Wyeomyia (*Dendromyia*) *brucei* of ?Cerqueira, 1943: 21 (Bolivia; collection record); Duret, 1949: 449, 450–451 (Argentina; ♀; collection record); Duret, 1950*b*: 314 (Argentina; list); Duret, 1951: 375 (Argentina; collection record); Castro *et al*., 1960: 560 (Argentina; collection record).

Dendromyia personata of Lane, 1936*b*: 181 (Brazil; A bionomics).

ADULT. As described for genus. Measurements in Table 1; numbers of setae in Table 2. *Thorax*: Postprocoxal scales usually present. Pleural scaling more white that silvery white.

FEMALE. Proboscis entirely dark-scaled, very dark (black). *Genitalia* (Fig. 10C-H): As illustrated; tergum IX with none or 1 seta on either side of midline; insula with 8 or 9 setae on either side; dorsal surface of postgenital lobe with 2–4 setae distally on either side of midline.

MALE. Proboscis (Fig. 2B,C) black-scaled dorsally; ventral surface white-scaled in distal 0.8, with brilliant blue iridescence in middle (0.40–0.65 from base) and slightly yellowish appearance distally. Maxillary palpus dark-scaled. *Genitalia* (Fig. 9G-L): Tergum IX without lobes, bearing 4–8(4) stout flattened setae on either side of midline, in more or less continuous row or only slightly separated at midline, apices of setae bent slightly laterad. Gonocoxite without distal tergal setal group; proximal group a tight cluster of 11–19 ($\bar{x} = 15$) very long slender setae (slightly shorter than gonocoxite). Basal mesal lobe with single long seta on caudal angle. Proctiger with 9–11(11) cercal setae.

PUPA (Figs 4A, 10). As described for genus; character and positions of setae as figured, numbers of branches in Table 5. *Cephalothorax*: Seta 1-CT variable, generally not noticeably sigmoidal; 10-CT usually single, sometimes forked apically. *Trumpet*: Length 0.29–0.42 mm ($\bar{x} = 0.36$ mm), pinna 0.02–0.12 mm ($\bar{x} = 0.07$ mm), width at mid-length 0.10–0.16 mm ($\bar{x} = 0.12$ mm), index 2.50–3.70 ($\bar{x} = 2.98$). *Abdomen*: Length 3.3–4.5 mm ($\bar{x} = 3.8$ mm). Seta 1-II usually triple (1–4); 6-VII noticeably stronger and longer than 5-VII, usually with few branches (3–10, mode 3). *Genital lobe*: Length about 0.35 mm in female, about 0.50 mm in male. *Paddle*: Length 0.54–0.66 mm ($\bar{x} = 0.60$ mm), width at widest point 0.37–0.50 mm ($\bar{x} = 0.43$ mm), index 1.32–1.62 ($\bar{x} = 1.41$).

LARVA (Figs 11,12). As described for genus; character and placement of setae as figured, numbers of branches in Table 6. Smaller than *On. personatum*. *Head*: Length 0.88–1.10 mm ($\bar{x} = 0.99$ mm); width 1.00–1.15 mm ($\bar{x} = 1.08$ mm). Dorsomentum with 9–12(11) teeth on either side of median tooth. Maxilla with 9–14(11) lateral teeth (laciniarastrum 1). *Antenna*: Length 0.26–0.30 mm ($\bar{x} = 0.28$ mm). *Abdomen*: Seta 1-IV,V double; 5-III–VI single. *Segment VIII*: Comb with 12–18(16) scales. *Siphon*: Length 1.28–1.48 mm ($\bar{x} = 1.39$ mm), width at base 0.25–0.31 mm ($\bar{x}$ = 0.27 mm), index 4.68–5.48 ($\bar{x}$ = 5.16); pecten with 94–129 filaments ($\bar{x}$ = 114). *Segment X*: Saddle length 0.26–0.34 mm ($\bar{x}$ = 0.30 mm); siphon/saddle index 4.26–5.35 ($\bar{x}$ = 4.67). Anal papillae very long, ventral pair about 4.5× length of saddle, dorsal pair shorter, about 0.7 length of ventral pair.

DISCUSSION. Because females of this species are indistinguishable from those of *On. celatum*, it is possible that the holotype female of *brucei* is conspecific with that species. Since available collections suggest that this species is distributed throughout a tract of land from southeastern Peru to northeastern Argentina, and because the name *brucei* was previously applied to specimens from the type locality of *Wy. belkini*, I have concluded that the species is likely to be represented by the holotype of *brucei*, and *belkini* is its junior synonym. This interpretation may be incorrect, but it is impossible to resolve the issue in the absence of diagnostic features in the females. This is further complicated by the possibility that the holotype of *brucei* may not be conspecific with either of the currently recognised species. *Onirion celatum* is only known from the type locality in southeastern Peru, approximately 1,600 km west-southwest of the type locality of *On. brucei*.

Onirion brucei shows a marked relationship to *On. aenigma* and *On. celatum*. Distal tergal setae are absent from the gonocoxites of these three species, and the genitalia of *On. brucei* and *On. aenigma* appear to be identical. Pupae of the last two species also resemble one another in the development of seta 6-VII, which is distinctly larger and generally has fewer branches than it has in other species of the genus. The only feature that distinguishes *On. brucei* from *On. aenigma* is the iridescent scaling of the proboscis in males. Males of *On. celatum* differ from those of *On. brucei* in having more extensive iridescent scaling on the proboscis and a single proximal tergal seta on the gonocoxites.

BIONOMICS. The type specimens of *On. brucei*, eleven females, were captured with human and unspecified animal bait (del Ponte & Cerqueira, 1938). Lane (1936*b*) captured females attracted to humans in forest at mid-day in August and September. The type specimens of *Wy. belkini* were collected as adults, apparently attracted to humans, and reared from larvae collected from bamboo internodes. Three adults examined during this study were reared from larvae found in perforated bamboo at the type locality of *Wy. belkini* (collection ARG511, see below); likewise, four larvae from Peru (Louton *et al.*, 1996) were collected from perforated bamboo internodes. Other specimens from Peru included in the material examined were taken from bamboo stumps and cut bamboo in association with unidentified species of *Culex* (*Carrollia*), *Culex* (*Melanoconion*), *Orthopodomyia*, *Trichoprosopon* and *Wyeomyia*. A single adult was captured in a malaise trap in rain forest. Nothing else is known about the bionomics of this species.

DISTRIBUTION. *Onirion brucei* is only definitely known from localities in extreme western Brazil (Mato Grosso), southeastern Peru and northeastern Argentina (Fig. 20C). Records of *On. personatum* in Bolivia (Cerqueira, 1943; Prosen *et al.*, 1963) probably refer to this species because it is likely to occur there. Some reports of *On. personatum* in extreme southern Brazil may also apply to this species. The species appears to be distributed from southeastern Peru eastward to the plateau of Mato Grosso and south-southeastward through Bolivia, Paraguay and northern Argentina, but the exact limits of its distribution are unknown.

MATERIAL EXAMINED.

Forty-six specimens (12♀, 6♂, 2♀G, 5♂G, 7Le, 7Pe, 7L), including seven individual rearings. *Holotype* ♀ of *Wyeomyia* (*Dendromyia*) *brucei* (4724), BRAZIL: *Mato Grosso*, Cuiabá, Junho 1935 (*G. Cesar*) (IOC). *Holotype* ♂ (C57) and *allotype* ♀ (C59) of *Wyeomyia* (*Dendromyia*) *belkini*, ARGENTINA: *Misiones*, Igu 26, 26-vi-1965 (*Hepper, García & Casal*) (INM). ARGENTINA: 3♀ 2♀G 1♂ 1♂G 1L, *Misiones*, Iguazú, Arroyo Ibicui, at Rt. 101 ~20 km from Cataratas del Iguazú, 5-v-1967 (2♀ 2♀G – ARG511-10, -11; 1♂ 1♂G – ARG511-12) (*O.H. Casal & M. Garcia*) (USNM), Deseado, 10.III.51 (1L – USNM; 1♀ – BMNH) (*Duret*); 1♀, *Corrientes*, Les Piedias, XII.66 (Duret) (USNM). BRAZIL: 4♀, *Mato Grosso*, Cuiabá, Fevereiro 1935 (1♀ – 3317), Pocinho, Agosto 1924 (1♀ – 3017), Ponce, Agosto 1934 (1♀ – 3017), Chapada, 600 m (1♀ – 324) (*Lane*) (USNM); 1♀, *Santa Catarina*, Nova Teutonia (27°11'S 52°23'W), 7.4.1937 (*F. Plaumann*) (BMNH). PERU: 2♀ 4♂ 3♂G 5Le 5Pe 6L, *Madre de Dios*, Rio Manu, Pakitza (11°55'48"S 71°15'18"W), 250 m, Sept. 89, water in *Guadua* bamboo, internode #37-3 (3L), internode #44-1 (1L) (*Louton, Bouchard & Gelhaus*) WRBU Acc. 1426 (USNM); same locality, 28 Oct 90 (1LPe♂ 1♂G – PE427-6), 29 Oct 90 (3LePe♂ 3♂G – PE433-2, -3, -4), 30 Oct 90 (1LePe♀ – PE457-2), 3 Nov 90 (1L – PE520), 7 Nov 90 (1L – PE623), 16 Nov 90 (1♀ – PE760) (*Wilkerson, Gaffigan & Mallampalli*) ACC 1445 (USNM).

Onirion celatum Peyton & Harbach, sp.n.

(Figs 2, 13–15)

ADULT. As described for genus. Measurements in Table 1; numbers of setae in Table 2. *Thorax*: Postprocoxal scales usually present. Pleural scaling generally silvery white.

FEMALE. Proboscis entirely dark-scaled. *Genitalia*

(Fig. 13C-E): As illustrated; tergum IX with 0–2 setae on either side of midline; insula with 7–9 setae on either side; dorsal surface of postgenital lobe with 1–4 setae distally on either side of midline.

MALE. Proboscis (Fig. 2D,E) mainly black-scaled, with shaggy appearance due to semi-erect scaling in proximal half; ventral surface with extensive white scaling concentrated in 4 patches, 3 between 0.2–0.6 from base and one apically, which become bright iridescent blue when viewed from anterior and anterolateral angles. Maxillary palpus dark-scaled. *Genitalia* (Fig. 15A-F): Tergum IX without lobes, bearing 7 or 8 strong flattened setae in continuous row, apices of setae bent slightly laterad. Gonocoxite without distal tergal setal group; proximal group represented by a single long seta (as long as gonocoxite). Basal mesal lobe without long seta on caudal angle. Proctiger with 6–11 cercal setae.

PUPA (Fig. 13). As described for genus; character and positions of setae as figured, numbers of branches in Table 7. *Cephalothorax*: Seta 1-CT moderately sigmoidal; 10-CT usually double, often triple, divided at base. *Trumpet*: Length 0.40–0.44 mm ($\bar{x}$ = 0.42 mm), pinna 0.08–0.11 mm ($\bar{x}$ = 0.09 mm), width at midlength 0.14–0.16 mm ($\bar{x}$ = 0.15 mm), index 2.56–2.93 ($\bar{x}$ = 2.73). *Abdomen*: Length 3.9–4.3 mm ($\bar{x}$ = 4.1 mm). Seta 1-II generally with more branches than other species (1–8, mode 5); 6-VII no longer than 5-VII, with 3–8(5) branches. *Genital lobe*: Length about 0.35 mm in female, about 0.50 mm in male. *Paddle*: Length 0.60–0.66 mm ($\bar{x}$ = 0.63 mm), width at widest point 0.48–0.50 mm ($\bar{x}$ = 0.49 mm), index 1.22–1.38 ($\bar{x}$ = 1.29).

LARVA (Fig. 14). As described for genus; character and placement of setae as figured, numbers of branches in Table 8. Smaller than *On. personatum*. *Head*: Length 1.06–1.18 mm ($\bar{x}$ = 1.12 mm); width 1.14–1.24 mm ($\bar{x}$ = 1.19 mm). Dorsomentum with 9–12(10) teeth on either side of median tooth. Maxilla with 10–13(12) lateral teeth (laciniarastrum 1). *Antenna*: Length 0.29–0.30 mm ($\bar{x}$ = 0.30 mm). *Abdomen*: Seta 1-IV,V double; 5-III–VI normally all single (5-IV double on one side of one specimen). *Segment VIII*: Comb with 13–22(20) scales. *Siphon*: Length 1.33–1.39 mm ($\bar{x}$ = 1.37 mm), width at base 0.28–0.29 mm ($\bar{x}$ = 0.28 mm), index 4.59–4.96 ($\bar{x}$ = 4.85); pecten with 99–118 filaments ($\bar{x}$ = 108). *Segment X*: Saddle length 0.29–0.30 mm ($\bar{x}$ = 0.29 mm); siphon/saddle index 4.43–4.79 ($\bar{x}$ = 4.65). Anal papillae short and stout, dorsal pair about length of saddle, ventral pair about 1.5× length of saddle.

ETYMOLOGY. This name *celatum*, Latin for 'concealed, hidden', was chosen for this species by E.L.P., perhaps because he thought it was *On. brucei* (as *Wy. belkini*) until he dissected the male genitalia.

DISCUSSION. This species appears to be derived from the same stock that gave rise to *On. brucei* and *On. aenigma*. These species are sympatric in Peru and distal tergal setae are absent from the gonocoxites of the males. Females of *On. celatum* are indistinguishable from those of *On. brucei*, but differ from those of *On. aenigma* in lacking a ventral streak of pale scales on the distal half of the proboscis. Pupae differ in the weaker development of seta 6-VII. Males are strikingly distinct from these and the other species of *Onirion* in the ornamentation of the proboscis and the presence of a single proximal tergal seta on the gonocoxites.

BIONOMICS. The type specimens of this species were collected as larvae in oily water contained in a bamboo internode perforated with a beetle hole. The specific collection site was partially shaded and located in primary rain forest. Nothing is known about the habits of the adults.

DISTRIBUTION. *Onirion celatum* is only known from the type locality in southeastern Peru (Fig. 20C). The species may be confined to the eastern piedmont of the Andes Mountains in southeastern Peru, northwestern Bolivia and Acre State in western Brazil bordering on Peru and Bolivia.

MATERIAL EXAMINED.
Twenty-two specimens (4♀, 2♂, 3♀G, 2♂G, 5Le, 6Pe), from six individual rearings. *Holotype*, ♂ (PE522-4), with LePe and dissected genitalia on separate microscope slides, PERU: *Madre de Dios*, Rio Manu, Pakitza (11°55'48"S 71°15'18"W), 30 Oct 90 (*Wilkerson, Gaffigan & Mallampalli*), ACC 1445 (USNM). *Paratypes*, 1Pe♀ (PE522-100 with dissected genitalia), 3LePe♀ 2♂G (PE522-1, -2 with dissected genitalia, -5 with dissected genitalia), 1LePe♂ with dissected genitalia (PE522-3), same data as holotype.

Onirion sirivanakarni (Duret)

(Figs 3, 13, 15)

1982. *Wyeomyia* (*Dendromyia*) *sirivanakarni* Duret, 1982: 167–170 (♂*). Holotype ♂, Darién, Panama (USNM); examined. **Comb.n.**

Wyeomyia (*Dendromyia*) *sirivanakarni* of Gaffigan & Ward, 1985: 62 (Panama; info. on type); Harbach *et al.*, 1991: 194 (Panama; info. on type); Ward, 1992: 207 (Panama; info. on type).

Wyeomyia (subgenus B) sp 52 of Heinemann & Belkin, 1978*a*: 193, 196 (Panama; collection record; L bionomics).

Wyeomyia sirivanakarni of Guimarães, 1997: 132 (Panama; info. on type).

Wyeomyia personata in part of Guimarães, 1997: 130 (?Colombia, Panama).

Wyeomyia (*Dendromyia*) *personata* in part of Arnett, 1949: 247–248 (Panama; distribution; L bionomics, bamboo joints only?); Stone *et al*., 1959: 86–87 (Panama); ?Barreto & Lee, 1969: 418 (Colombia; A bionomics); Knight & Stone, 1977: 330 (Panama).

ADULT. As described for genus. Measurements in Table 1; numbers of setae in Table 2. *Thorax*: Postprocoxal scales present, sometimes apparently absent. Pleural scaling generally silvery white.

FEMALE. Proboscis progressively swollen toward apex beginning 0.4 from base; dark-scaled except for slight indication of some pale scales ventrally at apex of prementum. *Genitalia* (Fig. 13F-H): As illustrated; tergum IX produced on either side of midline, each lobe with 4–11(8) setae; insula with 7–12 setae on either side; dorsal surface of postgenital lobe with 4–6 setae distally on either side of midline.

MALE. Proboscis (Fig. 3A,B) uniquely developed; mainly dark-scaled, with an enlarged (flared) section beginning 0.6 from base and bearing lateral tufts of long black scales 0.75 from base, ventral surface of enlarged area with long yellow scales; prementum narrower distal to lateral tufts, bearing creamy or yellowish scales of normal length ventrally and often turned upward with black tufts of enlarged section projecting anterolaterad at its base; yellow scaling of venter begins as narrow streak about 0.4–0.5 from base and rather abruptly broadens and scales lengthen in enlarged section. *Genitalia* (Fig. 15G-L): Tergum IX with widely separated lobes, each with 2 or 3 irregular rows of short stout setae and a single strong longer tapered seta, short setae decrease in length as they extend mesad onto long median bridge separating lobes. Gonocoxite with proximal and distal tergal setal groups; proximal group a partially double row of 7–11(9) long slender flexible setae (about 0.7 length of gonocoxite), contiguous with distal group; distal group a longitudinal row of 18–26 ($\bar{x} = 22$) slightly longer close-set setae. Basal mesal lobe with single stronger seta on caudal angle. Proctiger with 11–22 cercal setae.

LARVA. Unknown.

PUPA. Unknown.

DISCUSSION. The male of *On. sirivanakarni* is unusual because of the unique development of the proboscis and tergum IX of the genitalia. The genitalia are otherwise similar to those of *On. personatum* and *On. regale*, indicating that *On. sirivanakarni* is probably a specialised offshoot from the stock which also gave rise to these two species. Females of *On. sirivanakarni* differ conspicuously from the other species in the development of tergum IX.

BIONOMICS. The environment where the holotype male of this species was captured and what it was doing at the time of capture were not indicated in the original description (Duret, 1982). Published data indicate that personnel of the Gorgas Memorial Laboratory collected immature stages (denoted by GG in the material examined section) in terrestrial bromeliads (one specimen, GG108–109) and bamboo (Heinemann & Belkin, 1978*a*), but only the reared adults from these collections were available for study. Numbers identifying these specimens indicate that they may have been reared from pupae, but there are no associated pupal exuviae (and the dissected genitalia of four males are missing as well). The majority, if not all, of the information attributed to this species (as *Wy. personata*) by Arnett (1949) undoubtedly applies to species of other genera. Larvae are likely to breed in 'bamboo joints' but not in 'tree holes, coconut shells, and tin cans'. Arnett stated that 'adults were captured while biting, during the day' and the 'species breeds throughout the year and is common'. The biting activity of this species requires confirmation; and based on the paucity of available collections of *Onirion* species, it seems unlikely that *On. sirivanakarni* would be a 'common' species.

DISTRIBUTION. *Onirion sirivanakarni* is only known from collections made in the Darién of Panama (Fig. 20C). Females collected by Barreto & Lee (1969) in Colombia near the border with Panama may refer to this species.

MATERIAL EXAMINED.
Twenty-six specimens (13♀, 7♂, 3♀G, 3♂G). *Holotype*, ♂ (5862), with dissected genitalia on microscope slide, PANAMA: *Darién*, I.1958 (*Duret*) (USNM). *Non-types*, PANAMA: 13♀ 6♂ 3♀G 3♂G, *Darién*, Pucro, 'Paya Camp', 50 m, 6 Jul 58 (5♀ – GG105-105, -106, -109, -118, -119; 1♂ – GG105-122, dissected genitalia LU; 1♂ 1♂G – GG105-125) (*Gorgas Memorial Lab. personnel*); 8 Jul 58 (1♀ 1♀G – GG109-106; 1♀ – GG109-126; 3♂ – GG109-107, -111, -121, dissected genitalia LU; 1♂ 1♂G – GG109-125) (*Gorgas Memorial Lab. personnel*); Paya, 'Quebrada Murqui', 50 m, 9 Sept 58 (4♀ – GG117-102, -106, -111, -112; 1♀ 1♀G – GG117-105) (*Gorgas Memorial Lab. personnel*) (USNM); locality unknown, 7 Jul 58 (1♀ 1♀G – GG108-109) (*Gorgas Memorial Lab. personnel*) (USNM).

Onirion imparis Peyton & Harbach, sp.n.

(Figs 3, 16–18)

Wyeomyia (subgenus B) ?sp 34 of Heinemann & Belkin, 1978*b*: 380, 381, 396 (Venezuela; collection record; L bionomics).

Wyeomyia (subgenus B) sp 34 of Heinemann & Belkin, 1979: 97, 109 (Ecuador; collection record; L bionomics).

Wyeomyia personata in part of Cova Garcia *et al.*, 1966: 73 (Vol. I; 74, 353 = ♂ *On. personatum*), 68, 137, 313 (Vol. II) (Venezuela; ♀ L keys; collection record); Guimarães, 1997: 130 in part (?Colombia, Venezuela).

Wyeomyia (*Dendromyia*) *personata* of Lane, 1939: 146 in part (Venezuela record only, literature); Anduze *et al.*, 1947: 13 (Venezuela; list); Lane, 1953: 964 in part (Venezuela); Leví-Castillo, 1953: 42 (Ecuador; distribution); Stone *et al.*, 1959: 86–87 in part (Venezuela); ?Barreto & Lee, 1969: 418 (Colombia; A bionomics); Knight & Stone, 1977: 330 in part (?Colombia, Venezuela).

ADULT. As described for genus. Measurements in Table 1; numbers of setae in Table 2. *Thorax*: Postprocoxal scales present. Pleural scaling generally silvery white.

FEMALE. Proboscis entirely dark-scaled. *Genitalia* (Fig. 16C-E): As illustrated; tergum IX with 1 seta on either side of midline; insula with 6–8 setae on either side; dorsal surface of postgenital lobe with 4 or 5 setae distally on either side of midline.

MALE. Proboscis (Fig. 3C) thinner than other species of genus; slightly flattened and laterally expanded in distal third; ventral surface yellow-scaled as in *On. personatum*, duller yellow proximally and extended laterally and dorsally at base. Maxillary palpus same colour as base of proboscis. *Genitalia* (Fig. 18A-F): Tergum IX without lobes, bearing 8–14 rather long flattened setae in continuous row, setae shorter in middle of row, apices of setae bent laterad. Gonocoxite with widely separated proximal and distal tergal setal groups; proximal group a tight cluster of 28–34 ($\bar{x}$ = 30) long stiff setae with flexible ends (about 0.7 length of gonocoxite); distal group a short row of 8–11(9) slightly longer and thicker setae slightly bowed before mid-length. Basal mesal lobe without long seta on caudal angle. Proctiger with 18–33(24) cercal setae.

PUPA (Fig. 16). As described for genus; character and positions of setae as figured, numbers of branches in Table 9. Only one specimen known. *Cephalothorax*: Seta 1-CT strongly sigmoidal; 10-CT single. *Trumpet*: Length 0.37 mm, pinna 0.08 mm, width at mid-length 0.13 mm, index 2.85. *Abdomen*: Length 4.3 mm. Seta 1-II single/double; 6-VII shorter than 5-VII, with 5/4 branches. *Genital lobe*: Length (male) about 0.50 mm. *Paddle*: Length 0.65 mm, width at widest point 0.50 mm, index 1.30.

LARVA (Fig. 17). As described for genus; character and placement of setae as figured, numbers of branches in Table 10. Smaller than *On. personatum*. *Head*: Length 0.97–1.08 mm ($\bar{x}$ = 1.03 mm); width 1.21–1.23 mm ($\bar{x}$ = 1.22 mm). Dorsomentum with 10 or 11 teeth on either side of median tooth. Maxilla with 11 or 12(11) lateral teeth (laciniarastrum 1). *Antenna*: Length 0.29–0.30 mm. *Abdomen*: Seta 1-IV,V double; 5-III–VI normally single (5-IV double on one side in each of 2 specimens). *Segment VIII*: Comb with 11–16(14) scales. *Siphon*: Length 1.44–1.45 mm, width at base 0.29–0.31 mm ($\bar{x}$ = 0.30 mm), index 4.68–4.96 ($\bar{x}$ = 4.82); pecten with 110–129 filaments ($\bar{x}$ = 120). *Segment X*: Saddle length 0.30–0.31 mm; siphon/saddle index 4.65–4.83 ($\bar{x}$ = 4.74). Anal papillae short, dorsal pair about length of saddle, ventral pair about 1.5× length of saddle.

ETYMOLOGY. The name *imparis* is a Latin adjective (*impar, -is*) meaning ‘unequal, unlike, discordant’.

DISCUSSION. *Onirion imparis* appears to be derived from the same stock that gave rise to *On. personatum*, *On. sirivanakarni* and *On. aenigma*. It differs from these species in having the proximal and distal setal groups of the gonocoxites widely separated. The entirely dark-scaled proboscis of females more closely resembles the condition in *On. sirivanakarni*, i.e. a slight indication of some pale scales ventrally at apex. Females of *On. personatum* and *On. aenigma* have a ventral streak of pale scaling on the distal half of the proboscis.

BIONOMICS. Specimens from Ecuador were collected as adults in traps in tropical forest (Heinemann & Belkin, 1979). Specimens from Venezuela were collected as larvae in association with *Orthopodomyia albicosta* (Lutz), *Sabethes* (*Peytonulus*) *undosus* (Coquillett) and *Trichoprosopon pallidiventer* (Lutz). The larvae were found in turbid water contained in cut bamboo internodes (0.5 m above ground) in deep shade (Heinemann & Belkin, 1978*b*).

DISTRIBUTION. *Onirion imparis* is only known from localities where the type specimens were collection in Ecuador and Venezuela (Fig. 20C). Females collected by Barreto & Lee (1969) in Colombia near the border with Panama could belong to this species.

MATERIAL EXAMINED.

Twelve specimens (1♀, 7♂, 1♀G, 4♂G, 1Le, 1Pe, 1L), including one incomplete individual rearing. *Holotype*, ♂ (VZ261-102), with dissected genitalia on microscope slide, VENEZUELA: *Carabobo*, Puerto Cabello, Borburata (19PFM1454), 5 m, 24 Jul 69 (*J. Pulido & J. Valencia*) (USNM). *Paratypes*, VENEZUELA: 1♀ with dissected genitalia (VZ261-12), 2♂ (VZ261 with dissected genitalia, VZ261-16 with dissected genitalia LU), 1LePe (VZ261-1), same data as holotype; 1L (VZ274-2), *Aragua*, Ocumare de la Costa, Rio Cumboto 2 km S of junction of Rts 3 and 8 (19PFM3250), 60 m, 28 Jul 69 (*J. Pulido & J. Valencia* (USNM). ECUADOR: 4♂ (ECU8, 2 with dissected genitalia; 670123-14, -15 with dissected genitalia LU), *Napo*, Coca, confluence of Rio Coca and Rio Napo, 250 m, 23 Apr–12 May 65 (*L. E. Pena G*) (USNM).

Onirion regale Peyton & Harbach, sp.n.

(Figs 3, 4, 16, 18, 19)

Wyeomyia (subgenus B) sp 62 of Heinemann & Belkin, 1977: 263, 286 (Costa Rica; collection record; L bionomics).

Wyeomyia personata in part of ?Guimarães, 1997: 130 (Mexico).

Wyeomyia (*Dendromyia*) *personata* in part of ?Stone *et al.*, 1959: 86–87 (Mexico); ?Díaz Nájera, 1966: 64 (Mexico; collection record, A bionomics); ?Díaz Nájera & Vargas, 1973: 125 (Mexico; distribution); ?Knight & Stone, 1977: 330 (Mexico).

ADULT. As described for genus. Measurements in Table 1; numbers of setae in Table 2. *Thorax*: Postprocoxal scales absent. Pleural scaling generally silvery white.

FEMALE. Proboscis entirely dark-scaled. *Genitalia* (Fig. 16F-H): As illustrated; tergum IX with 3 setae on either side of midline; insula with 8–11 setae on either side; dorsal surface of postgenital lobe with 4 or 5 setae distally on either side of midline.

MALE. Similar to *On. personatum* but ventral pale scaling of proboscis (Fig. 3D) not as extensive in proximal half, may begin at base or at any point between base and mid-length. Maxillary palpus distinctly paler than base of proboscis in dorsal and lateral view. *Genitalia* (Fig. 18G-L): Tergum IX without lobes, with row of 13–15 rather long slender setae, row with very narrow gap at midline, setae progressively longer from gap outward, apices of setae bent laterad. Gonocoxite with proximal and distal tergal setal groups; proximal group a cluster of 20–31 ($\bar{x} = 25$) long slender flexible setae (about 0.75 length of gonocoxite), contiguous with distal group; distal group a longitudinal row of 19–23(23) thicker and much longer close-set setae (about 1.3 length of gonocoxite). Basal mesal lobe with single long seta on caudal angle. Proctiger with 9–13(9) cercal setae.

PUPA. Unknown.

LARVA (Fig. 19). As described for genus; character and placement of setae as figured, numbers of branches in Table 11. On average intermediate in size between *On. personatum* and other species. *Head*: Length 1.05–1.25 mm ($\bar{x} = 1.16$ mm); width 1.21–1.35 mm ($\bar{x} = 1.27$ mm). Dorsomentum with 10 or 11(10) teeth on either side of median tooth. Maxilla with 8–14(13) lateral teeth (laciniarastrum 1). *Antenna*: Length 0.31–0.33 mm ($\bar{x} = 0.32$ mm). *Abdomen*: Setae 1-IV,V and 5-III–VI double (5-III present on one side of each of 4 specimens examined, 3 double, one single). *Segment VIII*: Comb with 13–17(14) scales. *Siphon*: Length 1.25–1.38 mm ($\bar{x} = 1.31$ mm), width at base 0.28–0.31 mm ($\bar{x} = 0.30$ mm), index 4.19–4.46 ($\bar{x} = 4.38$); pecten with 113–121 filaments ($\bar{x} = 117$). *Segment X*: Saddle length 0.28–0.31 mm ($\bar{x} = 0.30$ mm); siphon/saddle index 4.26–4.60 ($\bar{x} = 4.41$). Ventral anal papillae about 3× length of saddle, dorsal pair shorter, about 0.7 length of ventral pair.

DISCUSSION. This species is a member of the Personatum Group. It appears to be most closely related to the nominate species but the male differs in the amount of pale scaling on the proboscis and the development of setae on tergum IX of the genitalia. The divergence of these two species appears to be due to vicariance.

ETYMOLOGY. The name *regale* is a Latin adjective (*regalis, -e*) meaning 'of a king, royal, regal'. It is chosen for no reason other than it is an appealing name.

BIONOMICS. The type specimens of *On. regale* were collected as larvae in association with a species of *Corethrella*, *Culex* (*Carrollia*) *babahoyensis* Leví-Castillo, *Sabethes* (*Peytonulus*) *identicus* Dyar & Knab, *Sa.* (*Pey.*) *hadrognathus* Harbach, *Sabethes* (*Sabethes*) *cyaneus* (Fabricius) and three species of *Wyeomyia*. The larvae were found in broken bamboo (1.3 m above ground) under deep shade in premontane wet forest. It is possible that records of *Wy. personata* collected from human bait at ground level and on platforms in forest in southern Mexico (Díaz Nájera, 1966) apply to this species, otherwise nothing is known about the bionomics of the adults.

DISTRIBUTION. *Onirion regale* is only definitely known from the type locality in Costa Rica (Fig. 20C). Records of *Wy. personata* collected in Chiapas, Tabasco and Veracruz States in southern Mexico (Díaz Nájera, 1966; Díaz Nájera & Vargas, 1973) could conceivably apply to this species.

MATERIAL EXAMINED.

Sixteen specimens (7♀, 6♂, 1♀G, 2♂G). *Holotype*, ♂ (CR423-49), with dissected genitalia on microscope slide, COSTA RICA: *Heredia*, Puerto Viejo, Finca La Selva (16PHG254), 100 m, 8 Aug 71 (*D. W. Heinemann*) (USNM). *Paratypes*, 7♀ (CR423-40, -42, -45, -47 with dissected genitalia, -48, -81, -83), 5♂ (CR423-41 with dissected genitalia LU, -43 with dissected genitalia, -44, -46 with dissected genitalia LU, -80), same data as holotype.

Onirion aenigma Harbach, sp.n.

(Figs 3, 20, 21)

ADULT. As described for genus. Measurements in Table 1; numbers of setae in Table 2. *Thorax*: Postprocoxal scales present.

FEMALE. Proboscis as in *On. personatum*, dark-scaled with streak of pale scales on distal half of ventral surface. Scaling of hypostigmal, subspiracular and postspiracular areas of mesopleuron more yellow than usual in only available female. *Genitalia*: Tergum IX with 2 setae on either side of midline; insula with 7 or 8 setae on either side; dorsal surface of postgenital lobe with 3 or 4 setae distally on either side of midline.

MALE. Proboscis (Fig. 3E) and maxillary palpus as in *On. personatum*. *Genitalia*: As illustrated for *On. brucei* (Fig. 9G-L); tergum IX without lobes, bearing 4 or 5 stout flattened setae on either side of narrow gap at midline, apices of setae bent slightly laterad. Gonocoxite without distal tergal setal group; proximal group a tight cluster of 16–26 very long slender setae (about 0.75 length of gonocoxite). Basal mesal lobe with single long seta on caudal angle. Proctiger with 5–11 cercal setae.

PUPA (Fig. 20). As described for genus; character and positions of setae as figured, numbers of branches in Table 12. Known from 3 specimens. *Cephalothorax*: Seta 1-CT sigmoidal; 10-CT single. *Trumpet*: Length 0.33–0.40 mm ($\bar{x}$ = 0.37 mm), pinna 0.05–0.10 mm ($\bar{x}$ = 0.07 mm), width at mid-length 0.12–0.14 mm ($\bar{x}$ = 0.13 mm), index 2.75–3.00 ($\bar{x}$ = 2.87). *Abdomen*: Length 3.5–4.3 mm ($\bar{x}$ = 3.8 mm). Seta 1-II with 3 or 4 branches, more often with 4; 6-VII noticeably stronger and longer than 5-VII, often triple (1–6). *Genital lobe*: Length about 0.30 mm in female, about 0.50 mm in male. *Paddle*: Length 0.54–0.62 mm ($\bar{x}$ = 0.57 mm), width at widest point 0.42–0.46 mm ($\bar{x}$ = 0.44 mm), index 1.22–1.35 ($\bar{x}$ = 1.29).

LARVA (Fig. 21). As described for genus; character and placement of setae as figured, numbers of branches in Table 13. Generally smaller than *On. personatum*. *Head*: Length 1.08–1.15 mm ($\bar{x}$ = 1.10 mm); width 1.14–1.28 mm ($\bar{x}$ = 1.21 mm). Dorsomentum with 10 or 11(10) teeth on either side of median tooth. Maxilla with 9–12(10) lateral teeth (laciniarastrum 1). *Antenna*: Length 0.28–0.30 mm ($\bar{x}$ = 0.29 mm). *Segment VIII*: Comb with 10–15(12) scales. *Siphon*: Length 1.24–1.32 mm ($\bar{x}$ = 1.28 mm), width at base 0.26–0.29 mm ($\bar{x}$ = 0.27 mm), index 4.55–4.77 ($\bar{x}$ = 4.67); pecten with 100–126 filaments ($\bar{x}$ = 111). *Segment X*: Saddle length 0.26–0.30 mm ($\bar{x}$ = 0.28 mm); siphon/saddle index 4.40–4.77 ($\bar{x}$ = 4.57). Anal papillae long, slender; dorsal pair only slightly shorter than ventral pair.

DISCUSSION. E.L. Peyton failed to recognise this new species because the male genitalia are virtually indistinguishable from those of *On. brucei*. *Onirion aenigma* was not recognised as a separate species until detailed study of available males revealed that the ornamentation of the proboscis is utterly different from that of *On. brucei*. The genitalia of *On. aenigma* are so similar to those of *On. brucei* that the illustrations of the latter species (Fig. 9G-L) are applicable to the former species as well. The setae of tergum IX are narrowly separated into lateral groups in the two available males of *On. aenigma*, but this is likely to prove unreliable for distinguishing the two species once additional material is collected and studied.

Based on the structure of the male genitalia, *On. aenigma* is clearly a member of the Brucei Group. The ornamentation of the proboscis is puzzling because it resembles that of *On. personatum* and *On. imparis* of the Personatum Group.

ETYMOLOGY. The name *aenigma* is a Latin neuter noun meaning 'a riddle, mystery'. It was chosen because of the mystifying similarity of the male genitalia to those of *On. brucei*.

BIONOMICS. The type specimens of this species were collected as larvae from a bamboo internode perforated with a beetle hole. The collection also included unidentified species of *Culex* and *Wyeomyia*. The collection site was partially shaded and located in primary rain forest. Nothing is known about the bionomics of the adults.

DISTRIBUTION. *Onirion aenigma* is only known from the type locality in southeastern Peru (Fig. 20C).

MATERIAL EXAMINED.
Twelve specimens (1♀, 2♂, 1♀G, 2♂G, 3Le, 3Pe), from three individual rearings. *Holotype*, ♂ (PE454-7), with LePe and dissected genitalia on separate microscope slides, PERU: *Madre de Dios*, Rio Manu, Pakitza (11°55'48"S 71°15'18"W), 30 Oct 90, (*Wilkerson, Gaffigan & Mallampalli*), ACC 1445 (USNM). *Paratypes*, 1LePe♀ with dissected genitalia (PE454-5), 1LePe♂ with dissected genitalia (PE454-6), same data as holotype.

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Abbreviations used in figures

A	= antenna
AT	= apical tooth
C	= cranium
Ce	= cercus
CS	= comb scale
CT	= cephalothorax
Dm	= dorsomentum
dts	= distal tergal setae (of gonocoxite)
LR	= laciniarastrum
M	= mesothorax
MPlp	= maxillary palpus
MxB	= maxillary brush
MxBo	= maxillary body
P	= prothorax
Pa	= paddle
PGL	= postgenital lobe
pts	= proximal tergal setae (of gonocoxite)
S	= siphon
T	= metathorax
I–X	= abdominal segments
1–15	= setal numbers for specified areas

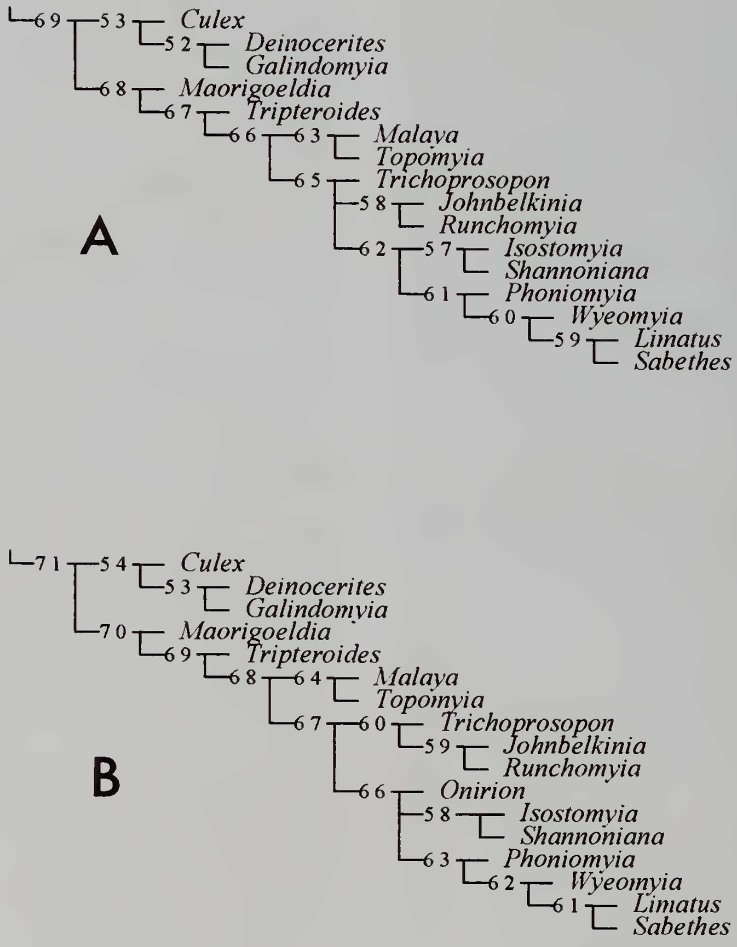

Fig. 1. A, Clade comprised of Culicini + Sabethini from the preferred cladogram of Harbach & Kitching (1998); B, altered topology of this clade when *Onirion* was added to the dataset (Appendices 1 and 2).

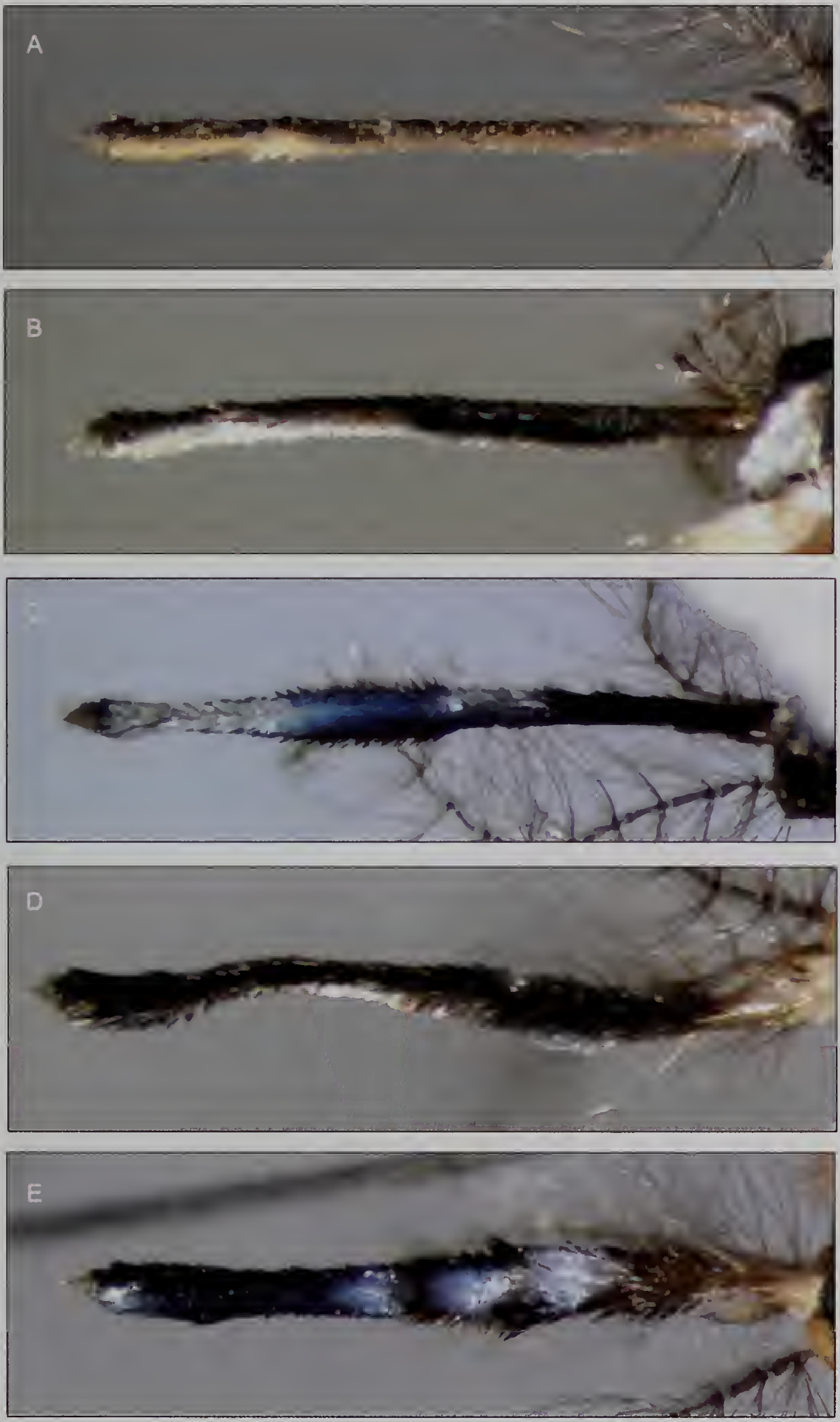

Fig. 2. Proboscises of *Onirion* males. A, *Onirion personatum* (left side); B,C, *On. brucei* (left side and ventral surface, respectively); D,E, *On. celatum* (left side and ventral surface, respectively).

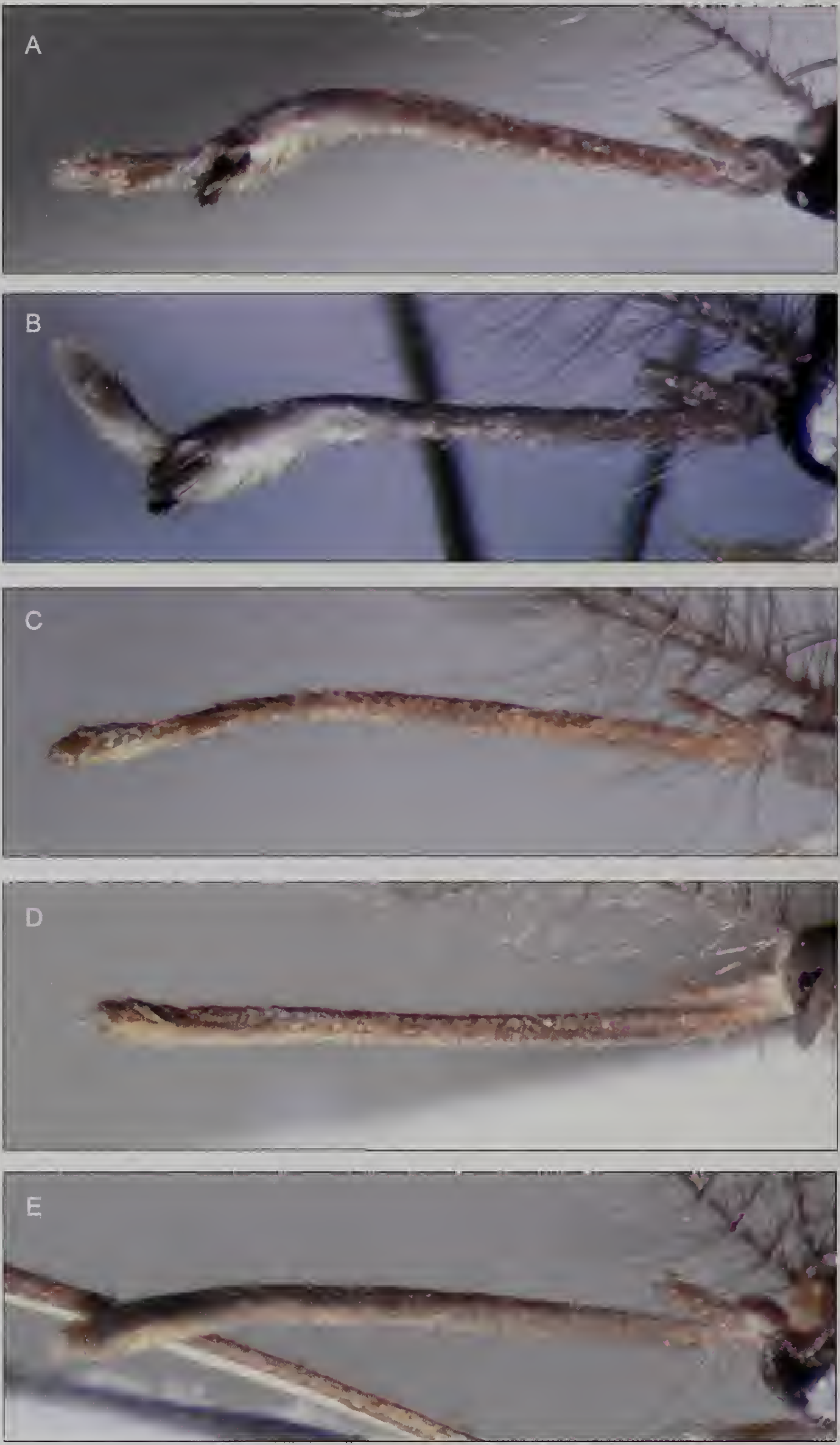

Fig. 3. Proboscises of *Onirion* males. A,B, *Onirion sirivanakarni* (left side); C, *On. imparis* (left side); D, *On. regale* (left side); E, *On. aenigma* (left side).

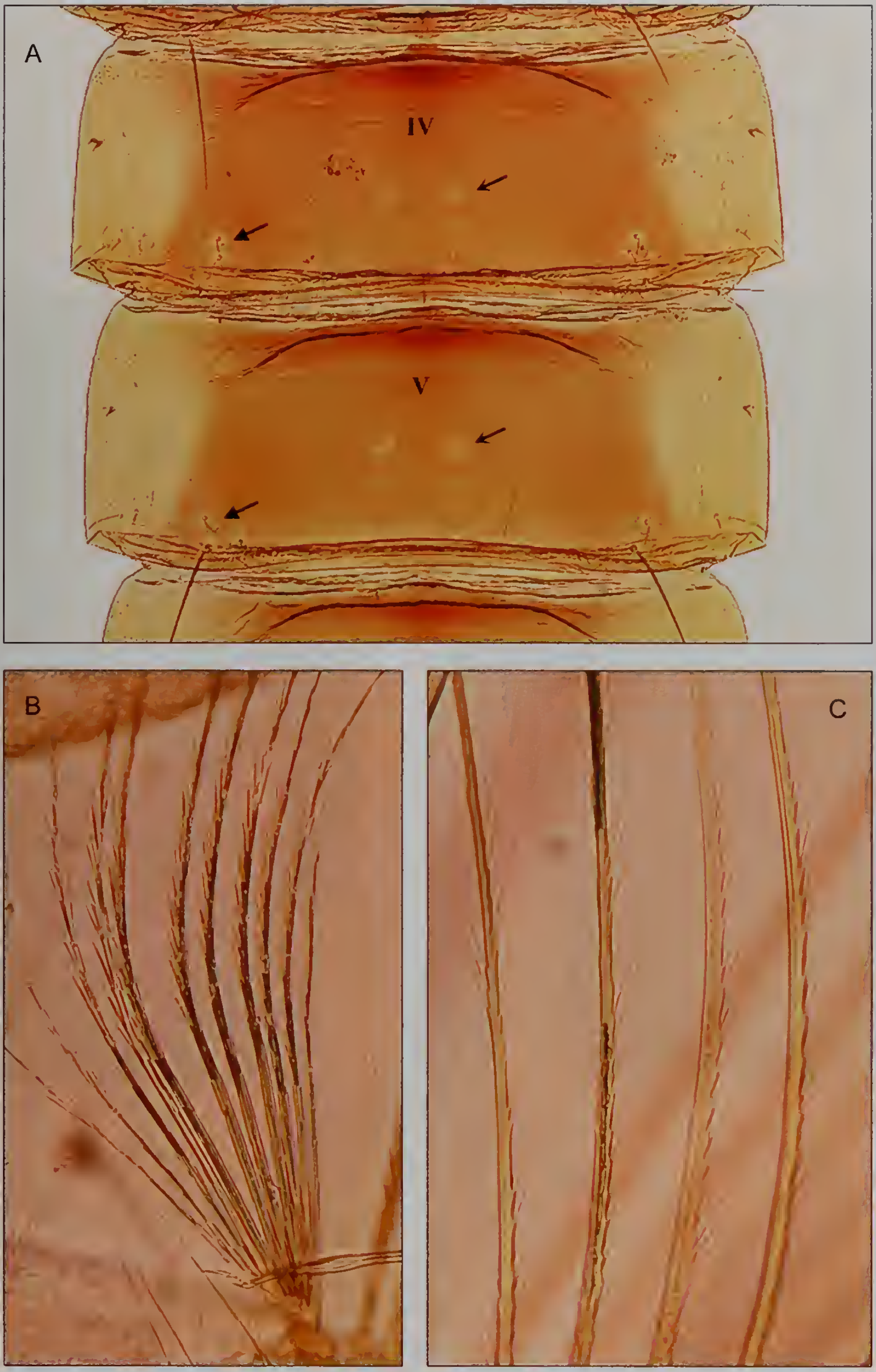

Fig. 4. Pupal and larval features characteristic of *Onirion*. A, Terga IV and V of pupa of *On. brucei* showing pattern of pigmentation, submedial scar-like depressions (arrows at right) and lack of pigment around bases of setae (arrows at left); B,C, setae 4-P (right side, *On. regale*) and 7-T (left side, *On. brucei*), respectively, showing preponderance of aciculae on one side of the branches.

Fig. 5. Female (left side) of *Onirion personatum* showing the ornamentation characteristic of all species of the genus.

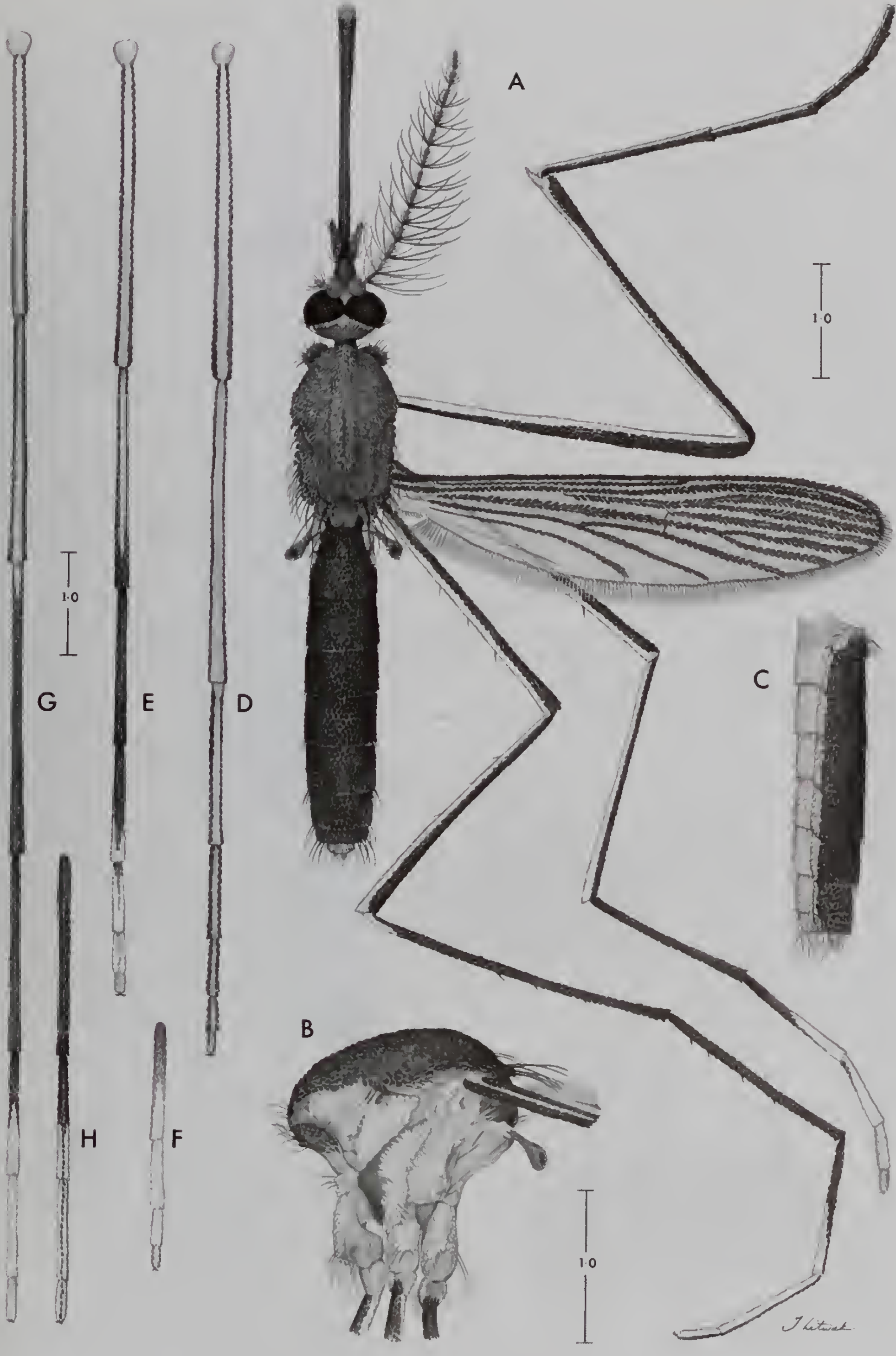

Fig. 6. Habitus of *Onirion personatum* female showing the pattern of dark and pale scaling characteristic of all species of the genus. A, Dorsal aspect of body and right wing, with anterior view of foreleg and posterior views of mid- and hindlegs; B, lateral (left side) of thorax; C, lateral (left side) of abdomen; D, foreleg (ventral); E,F, midleg (E, ventral; F, dorsal surface of tarsomeres 2–5); G,H, hindleg (G, ventral; H, dorsal surface of tarsomeres 2–5). Scales in mm.

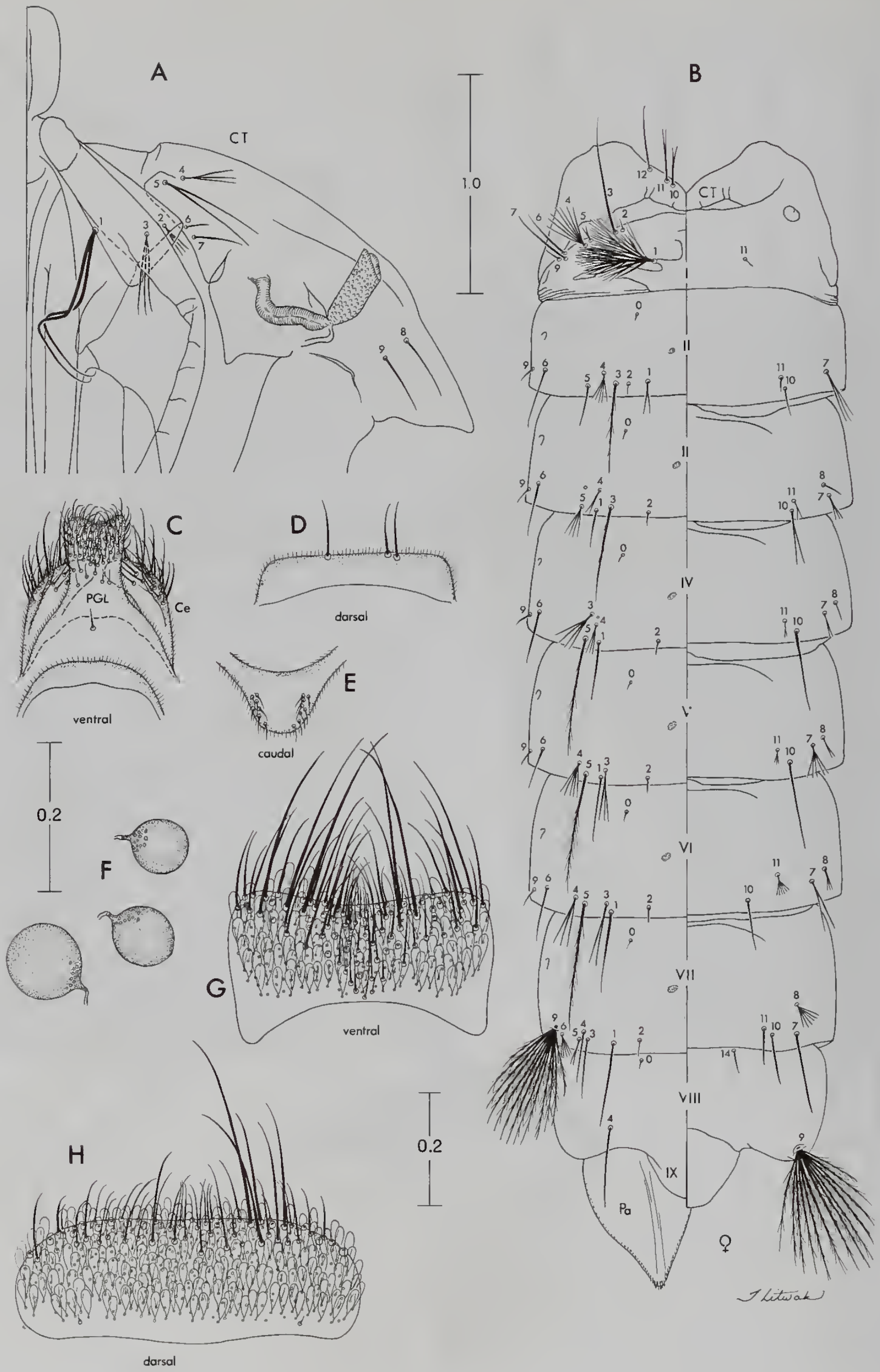

Fig. 7. Pupa and female genitalia of *Onirion personatum*. A,B, Pupa: (A) left side of cephalothorax, dorsal to right; (B) dorsal (left) and ventral (right) aspects of metathorax and abdomen. C-H, Female genitalia, aspects as indicated: (C) postgenital lobe and cerci; (D) tergum IX; (E) insula; (F) spermathecal capsules; (G) sternum VIII; (H) tergum VIII. Scales in mm.

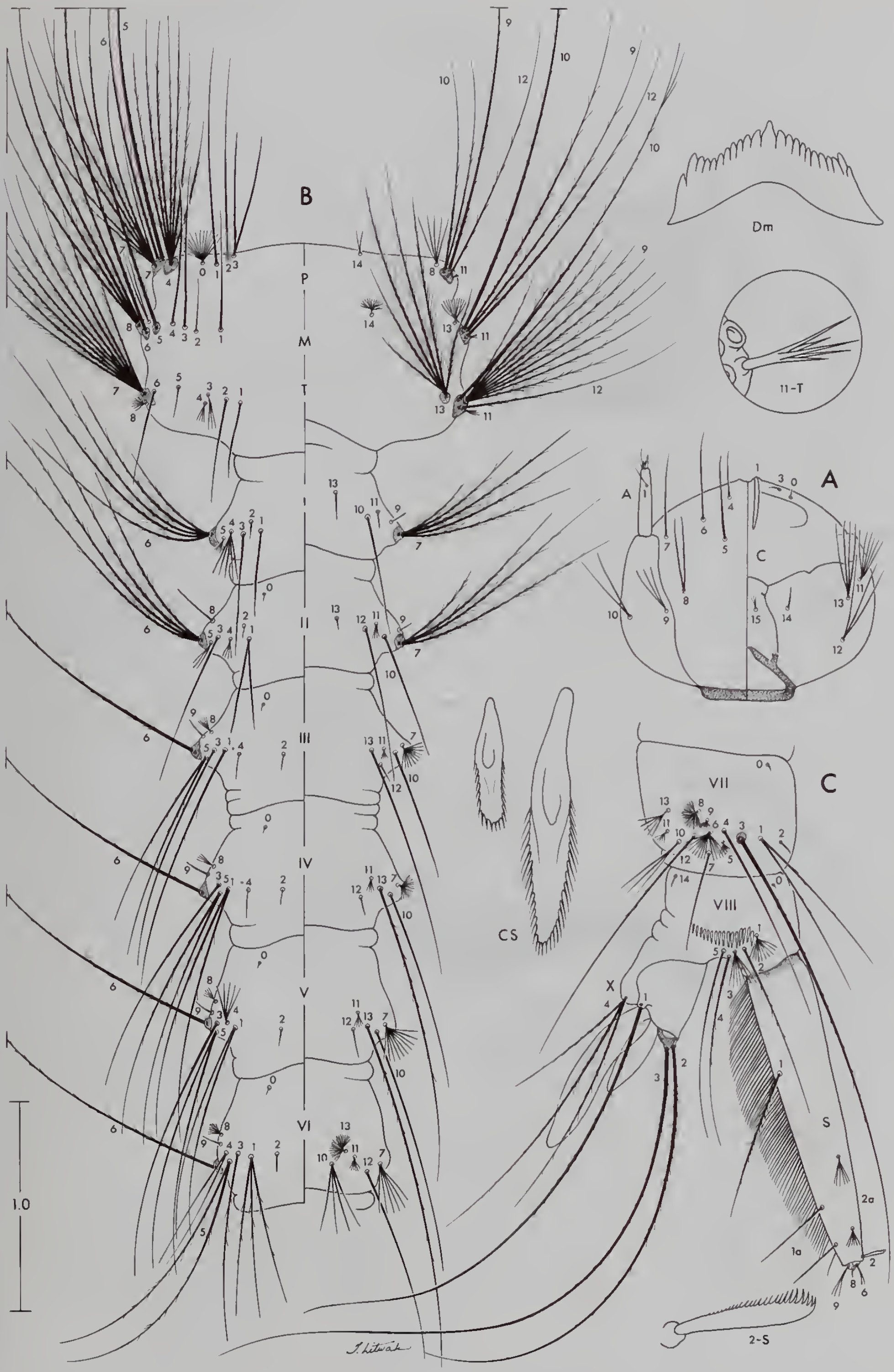

Fig. 8. Fourth-instar larva of *Onirion personatum*, reconstructed from exuviae. A, Head, dorsal and ventral aspects of left side; B, thorax and abdominal segments I–VI, dorsal and ventral aspects of left side; C, abdominal segments VII–X, left side. Scale in mm.

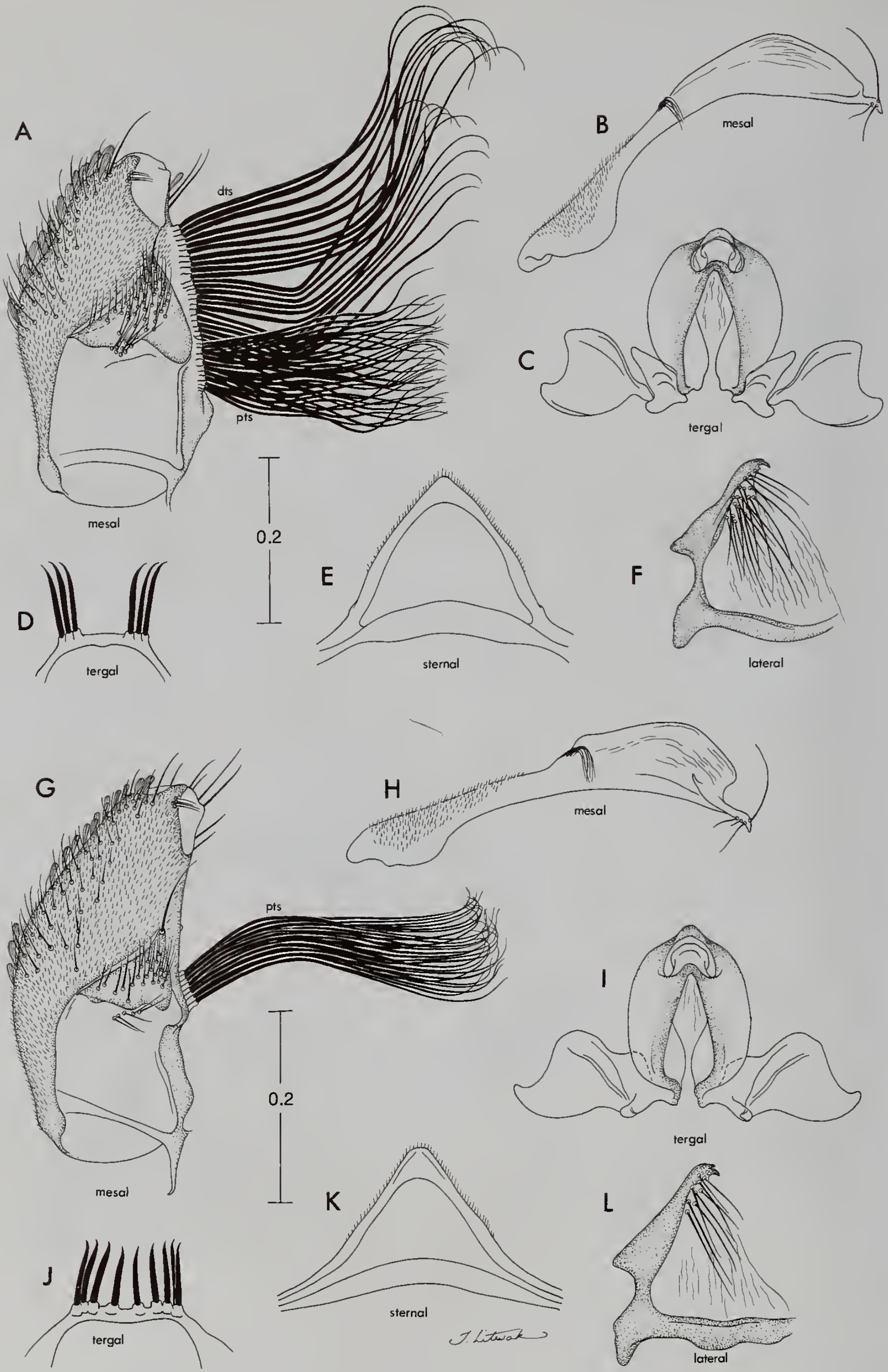

Fig. 9. Male genitalia of *On. personatum* (A-F) and *On. brucei* (G-L), aspects as indicated: (A,G) gonocoxite; (B,H) gonostylus; (C,I) aedeagus, with parameres and basal pieces attached; (D,J) tergum IX; (E,K) sternum IX; (F,L) proctiger (left side). Scales in mm.

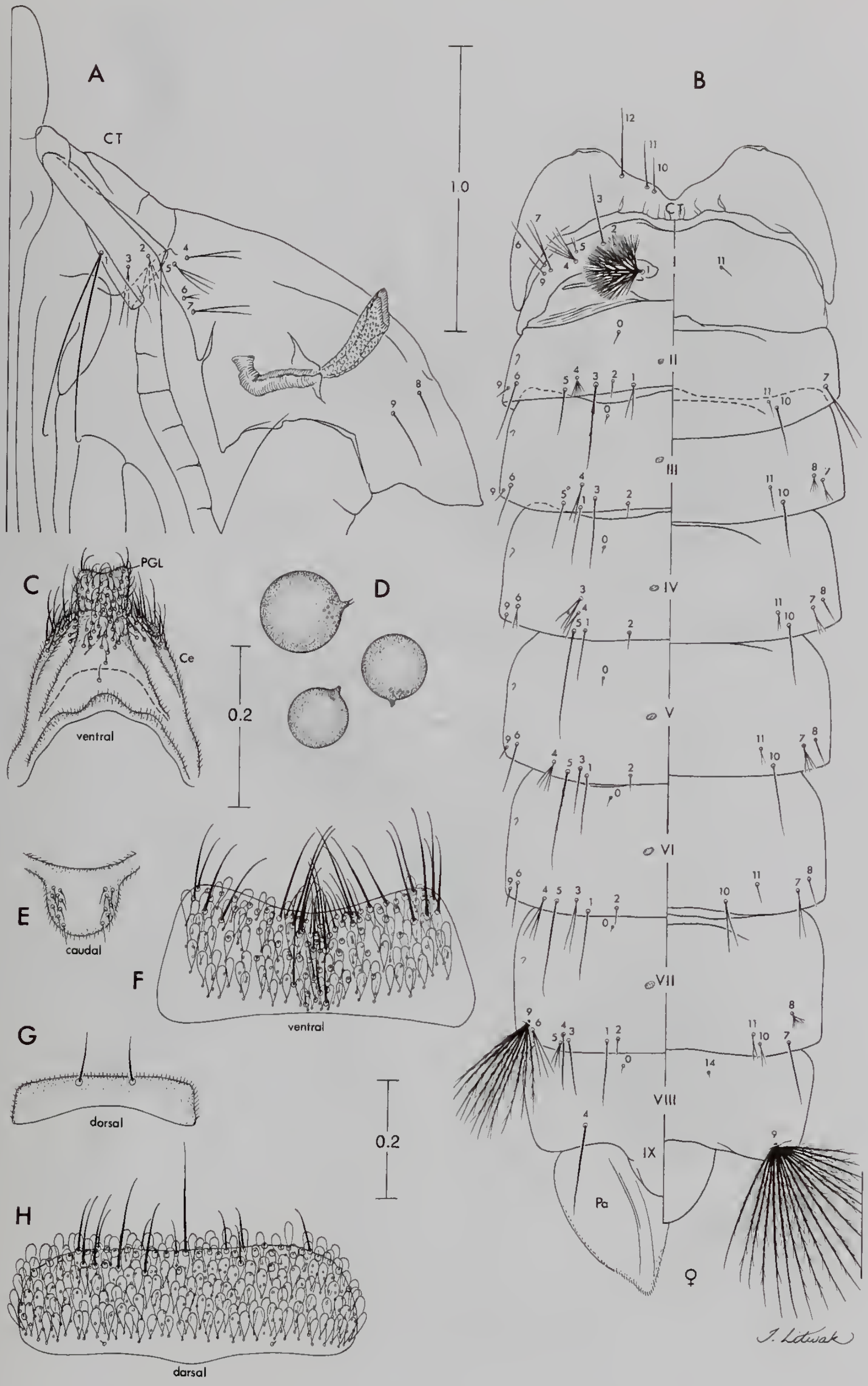

Fig. 10. Pupa and female genitalia of *Onirion brucei*. A,B, Pupa: (A) left side of cephalothorax, dorsal to right; (B) dorsal (left) and ventral (right) aspects of metathorax and abdomen. C-H, Female genitalia, aspects as indicated: (C) postgenital lobe and cerci; (D) spermathecal capsules; (E) insula; (F) tergum VIII; (G) tergum IX; (H) sternum VIII. Scales in mm.

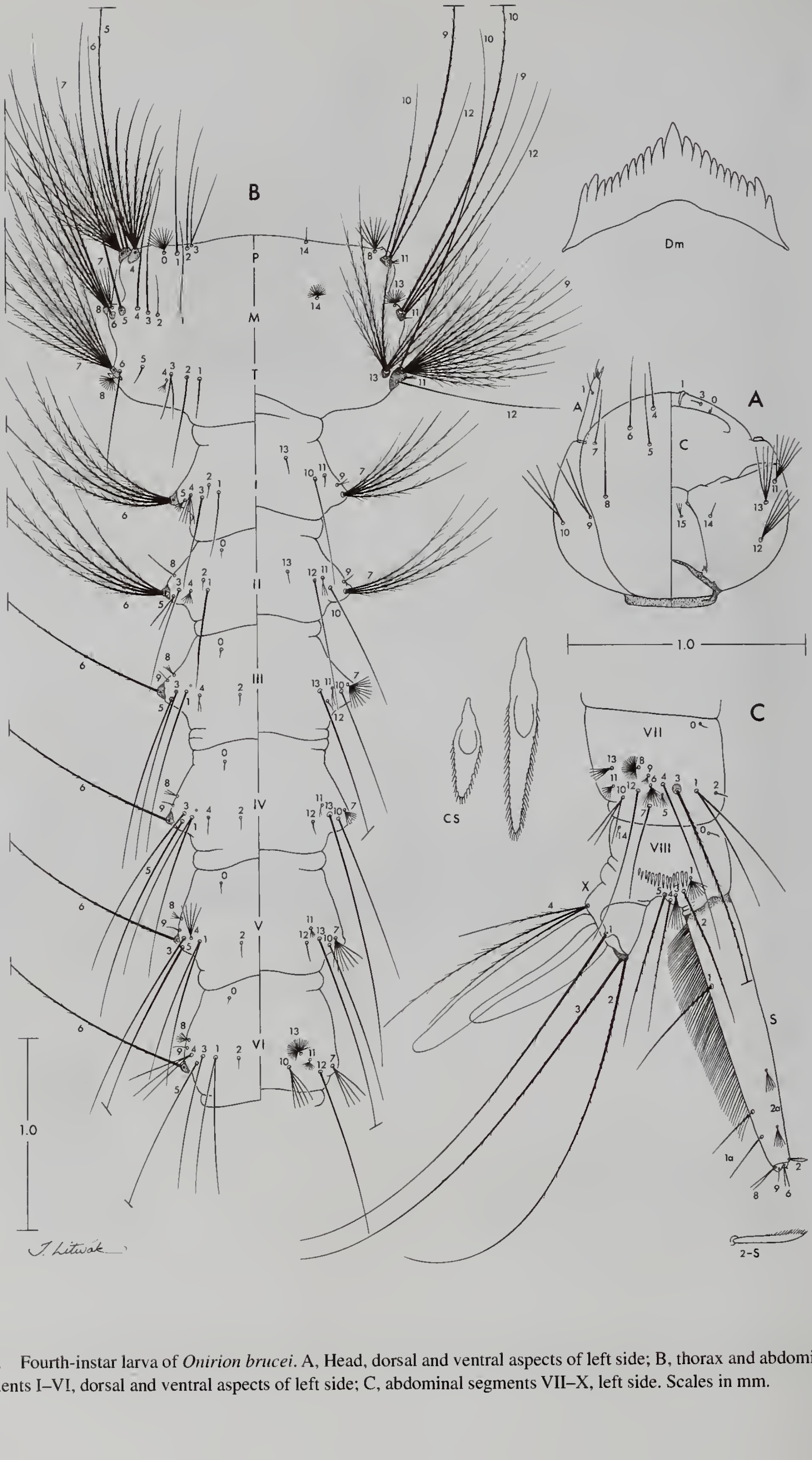

Fig. 11. Fourth-instar larva of *Onirion brucei*. A, Head, dorsal and ventral aspects of left side; B, thorax and abdominal segments I–VI, dorsal and ventral aspects of left side; C, abdominal segments VII–X, left side. Scales in mm.

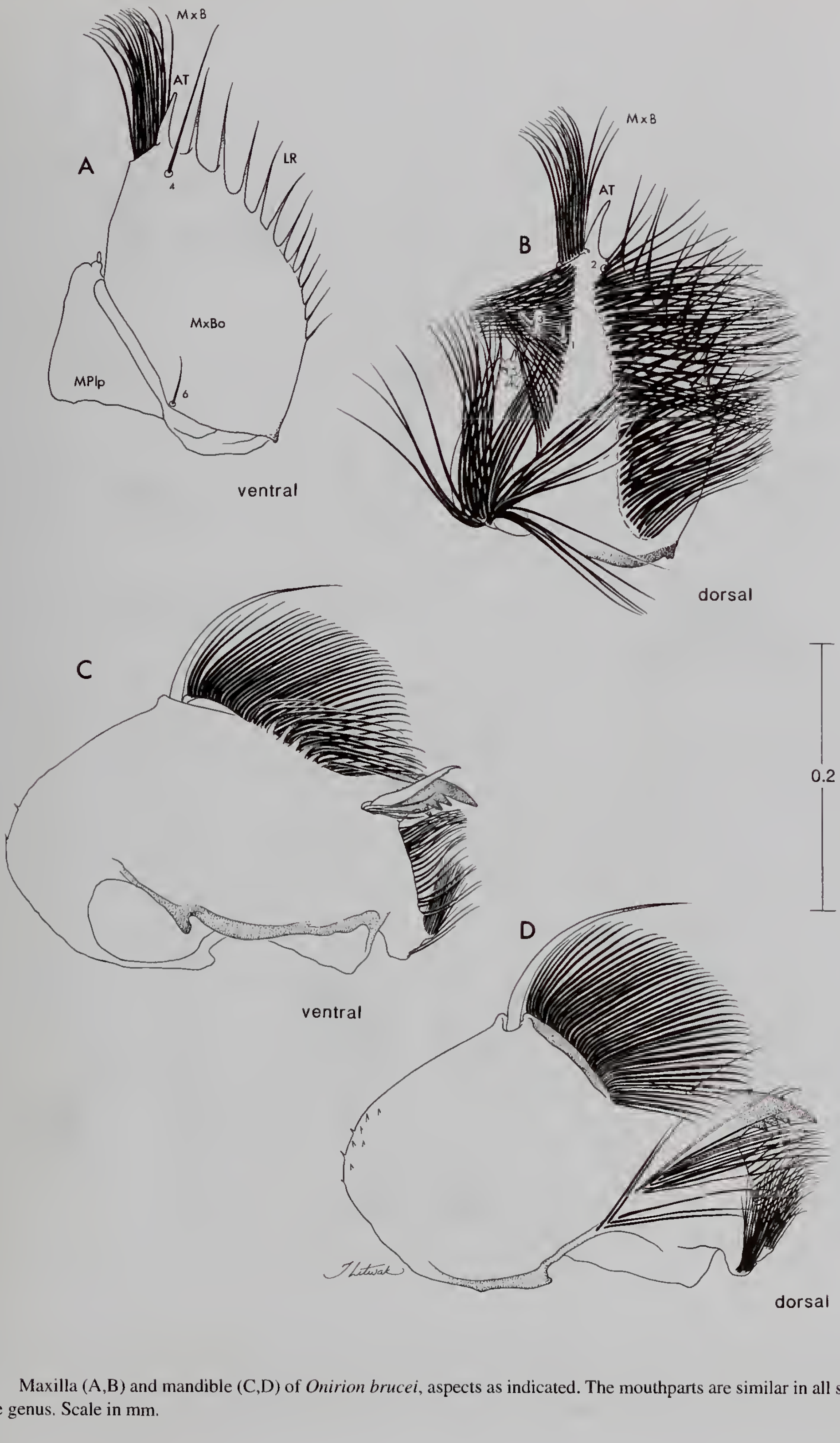

Fig. 12. Maxilla (A,B) and mandible (C,D) of *Onirion brucei*, aspects as indicated. The mouthparts are similar in all species of the genus. Scale in mm.

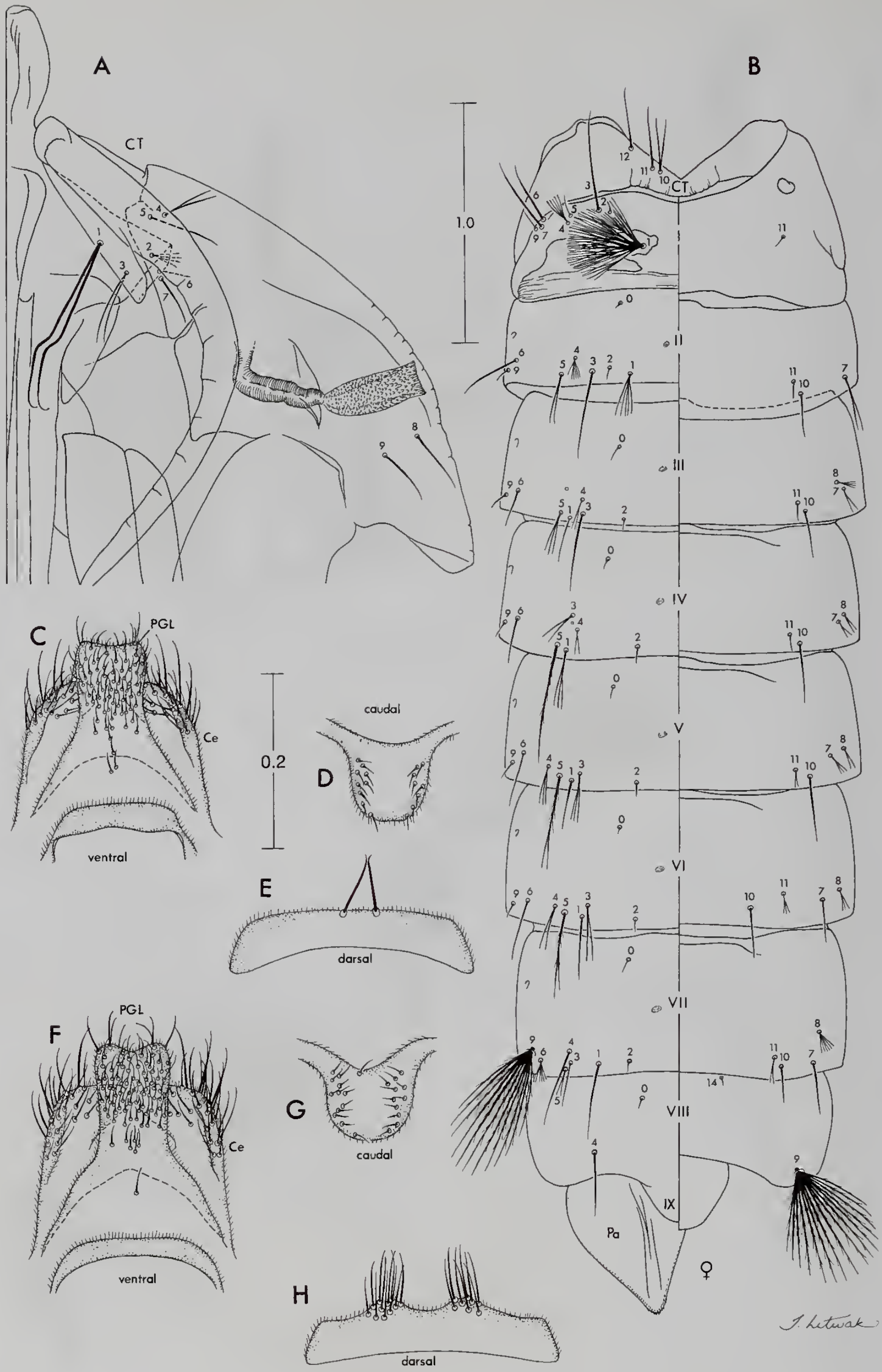

Fig. 13. A,B, Pupa of *Onirion celatum*: (A) left side of cephalothorax, dorsal to right; (B) dorsal (left) and ventral (right) aspects of metathorax and abdomen. C-H, Female genitalia of *On. celatum* (C-E) and *On. sirivanakarni* (F-H), aspects as indicated: (C,F) postgenital lobe and cerci; (D,G) insula; (E,H) tergum IX. Scales in mm.

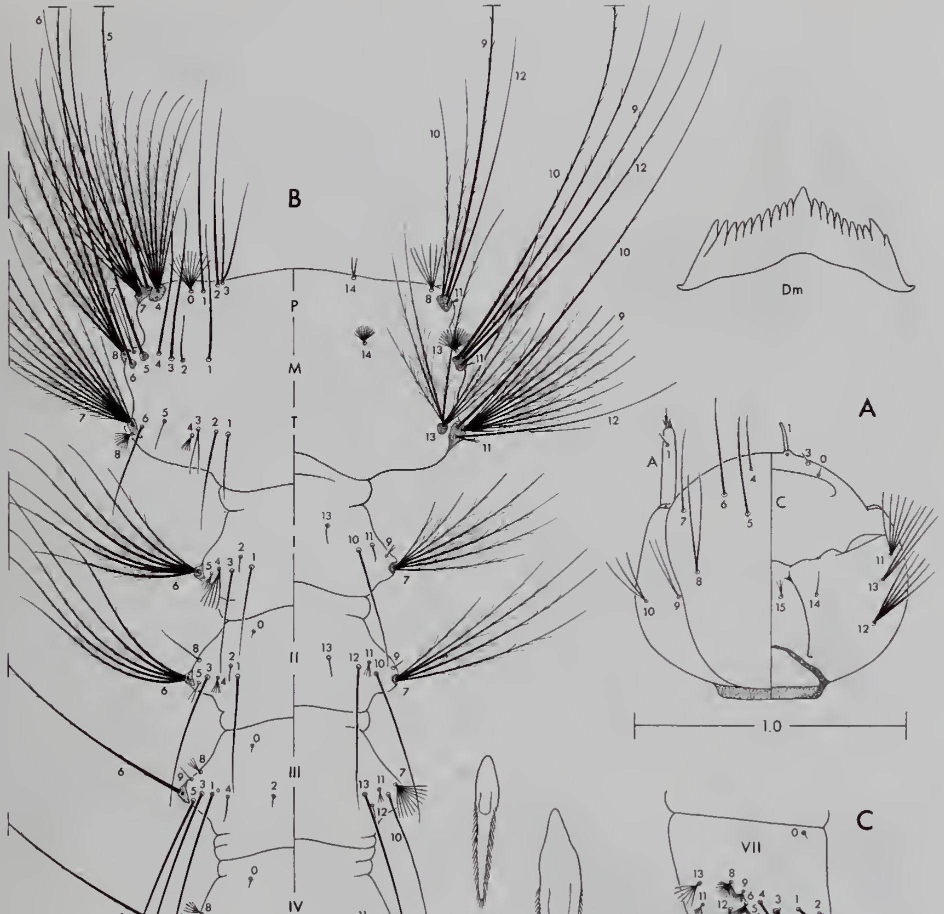

Fig. 14. Fourth-instar larva of *Onirion celatum*, reconstructed from exuviae. A, Head, dorsal and ventral aspects of left side; B, thorax and abdominal segments I–VI, dorsal and ventral aspects of left side; C, abdominal segments VII–X, left side. Scales in mm.

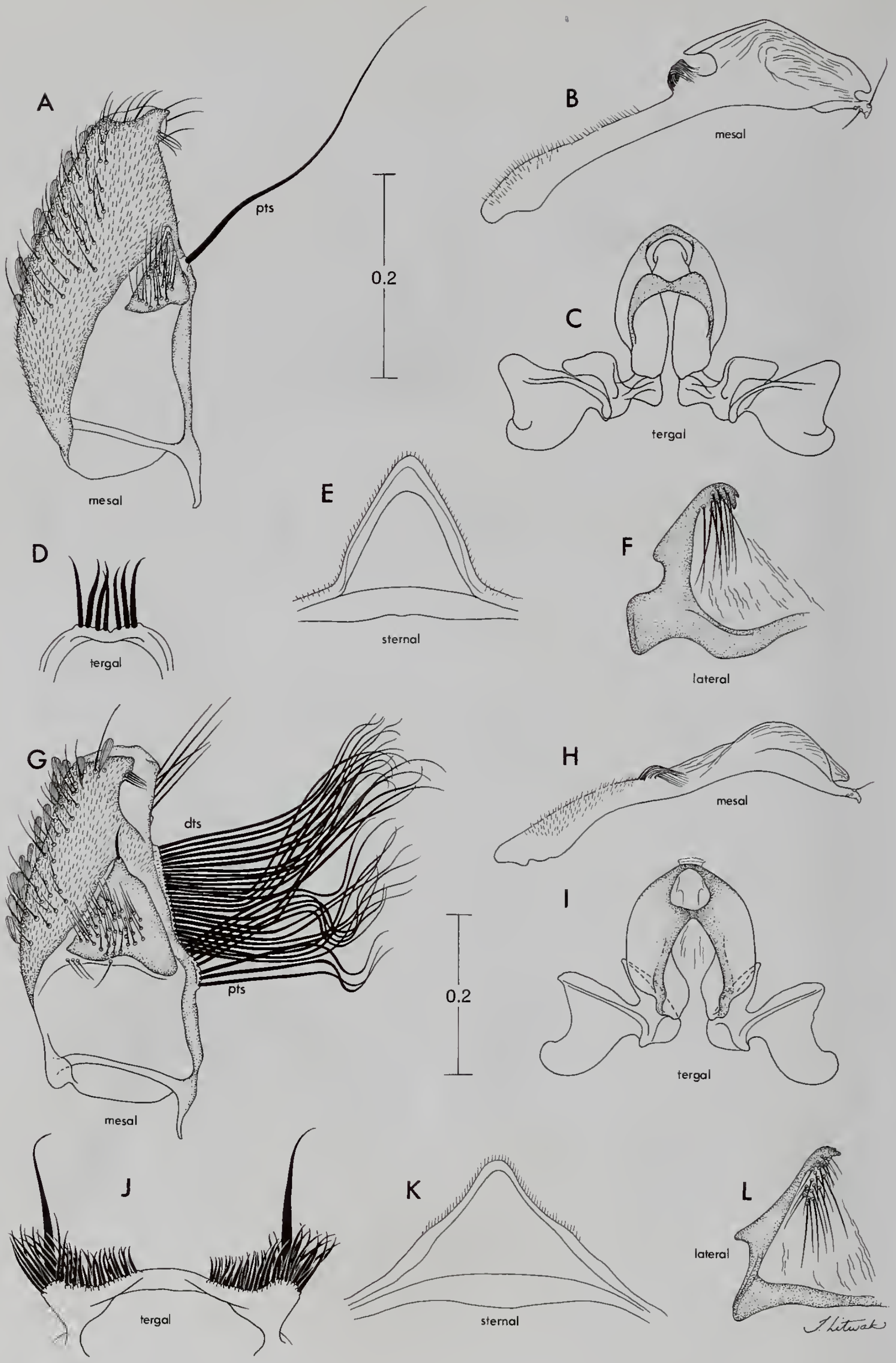

Fig. 15. Male genitalia of *On. celatum* (A-F) and *On. sirivanakarni* (G-L), aspects as indicated: (A,G) gonocoxite; (B,H) gonostylus; (C,I) aedeagus, with parameres and basal pieces attached; (D,J) tergum IX; (E,K) sternum IX; (F,L) proctiger (left side). Scales in mm.

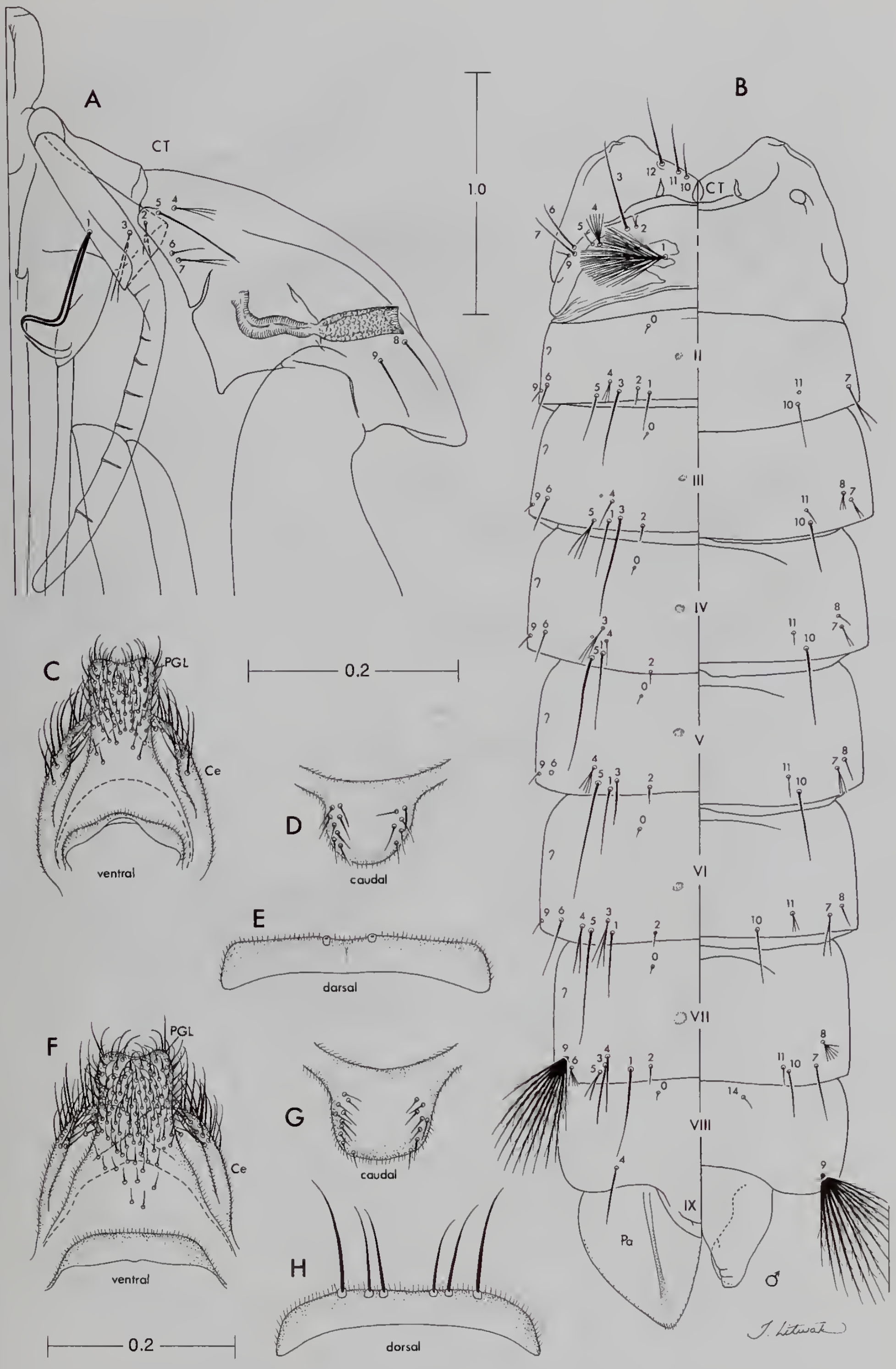

Fig. 16. A,B, Pupa of *Onirion imparis*: (A) left side of cephalothorax, dorsal to right; (B) dorsal (left) and ventral (right) aspects of metathorax and abdomen. C-H, Female genitalia of *On. imparis* (C-E) and *On. regale* (F-H), aspects as indicated: (C,F) postgenital lobe and cerci; (D,G) insula; (E,H) tergum IX. Scales in mm.

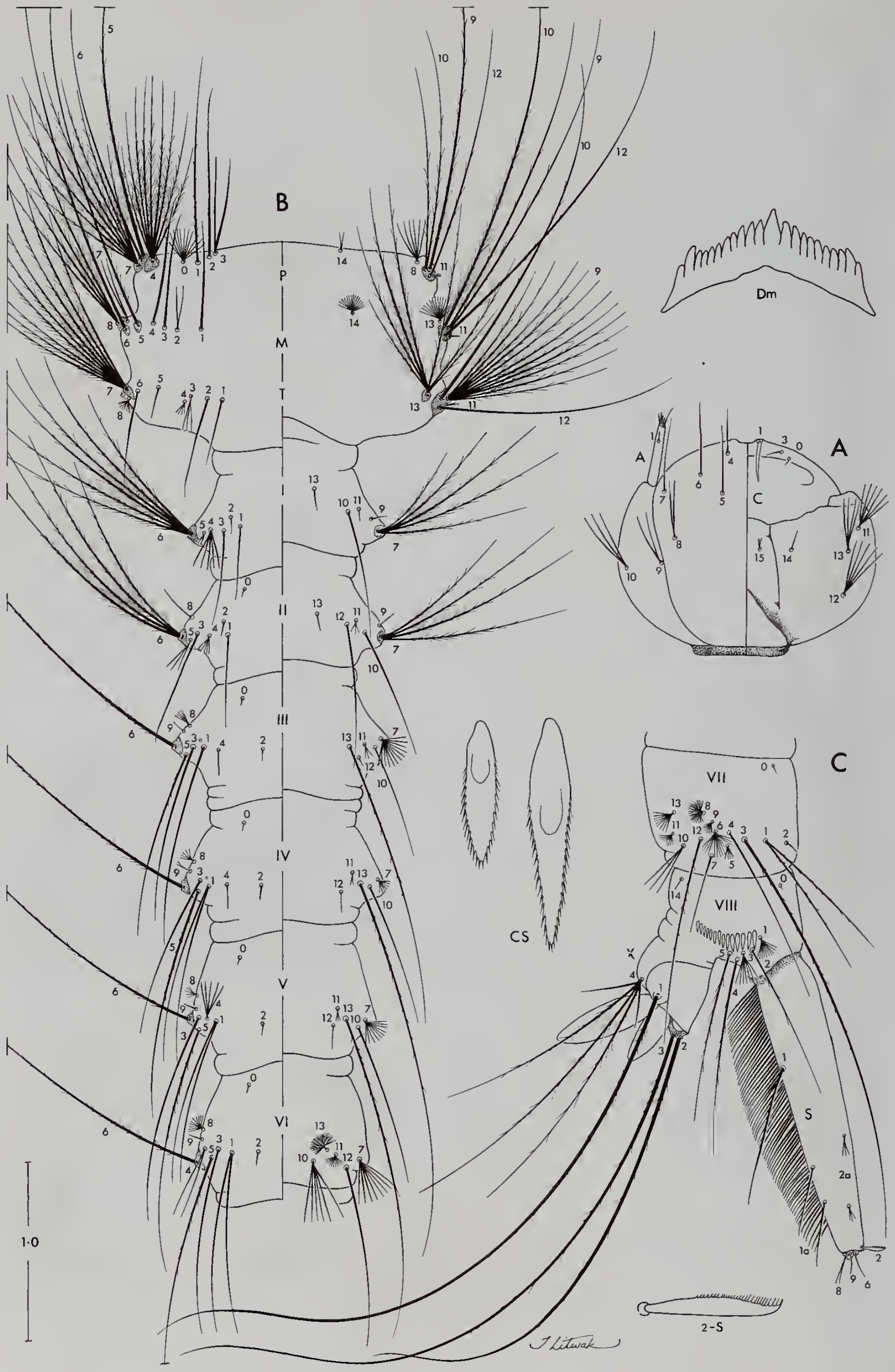

Fig. 17. Fourth-instar larva of *Onirion imparis*. A, Head, dorsal and ventral aspects of left side; B, thorax and abdominal segments I–VI, dorsal and ventral aspects of left side; C, abdominal segments VII–X, left side. Scale in mm.

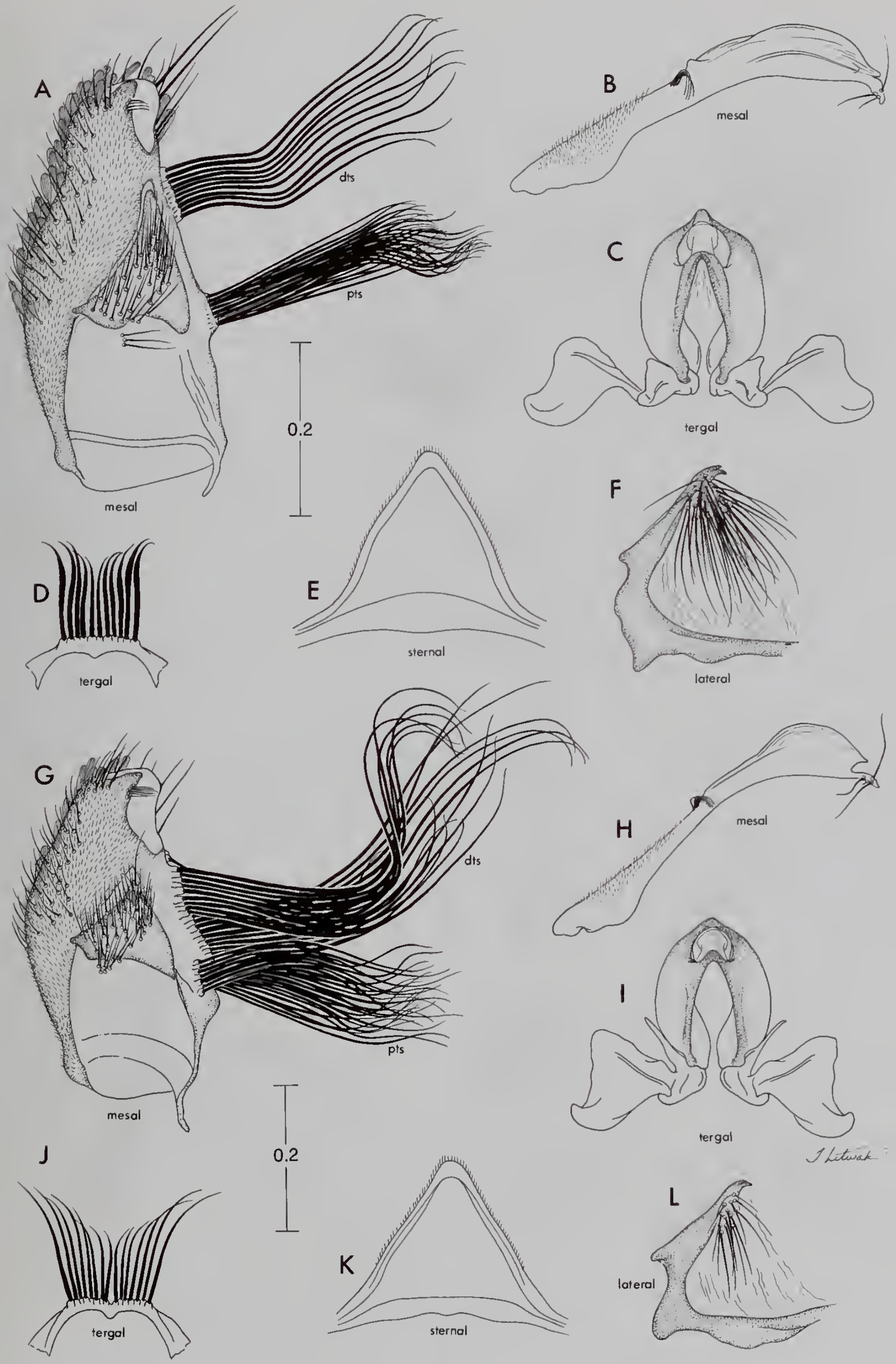

Fig. 18. Male genitalia of *On. imparis* (A-F) and *On. regale* (G-L), aspects as indicated: (A,G) gonocoxite; (B,H) gonostylus; (C,I) aedeagus, with parameres and basal pieces attached; (D,J) tergum IX; (E,K) sternum IX; (F,L) proctiger (left side). Scales in mm.

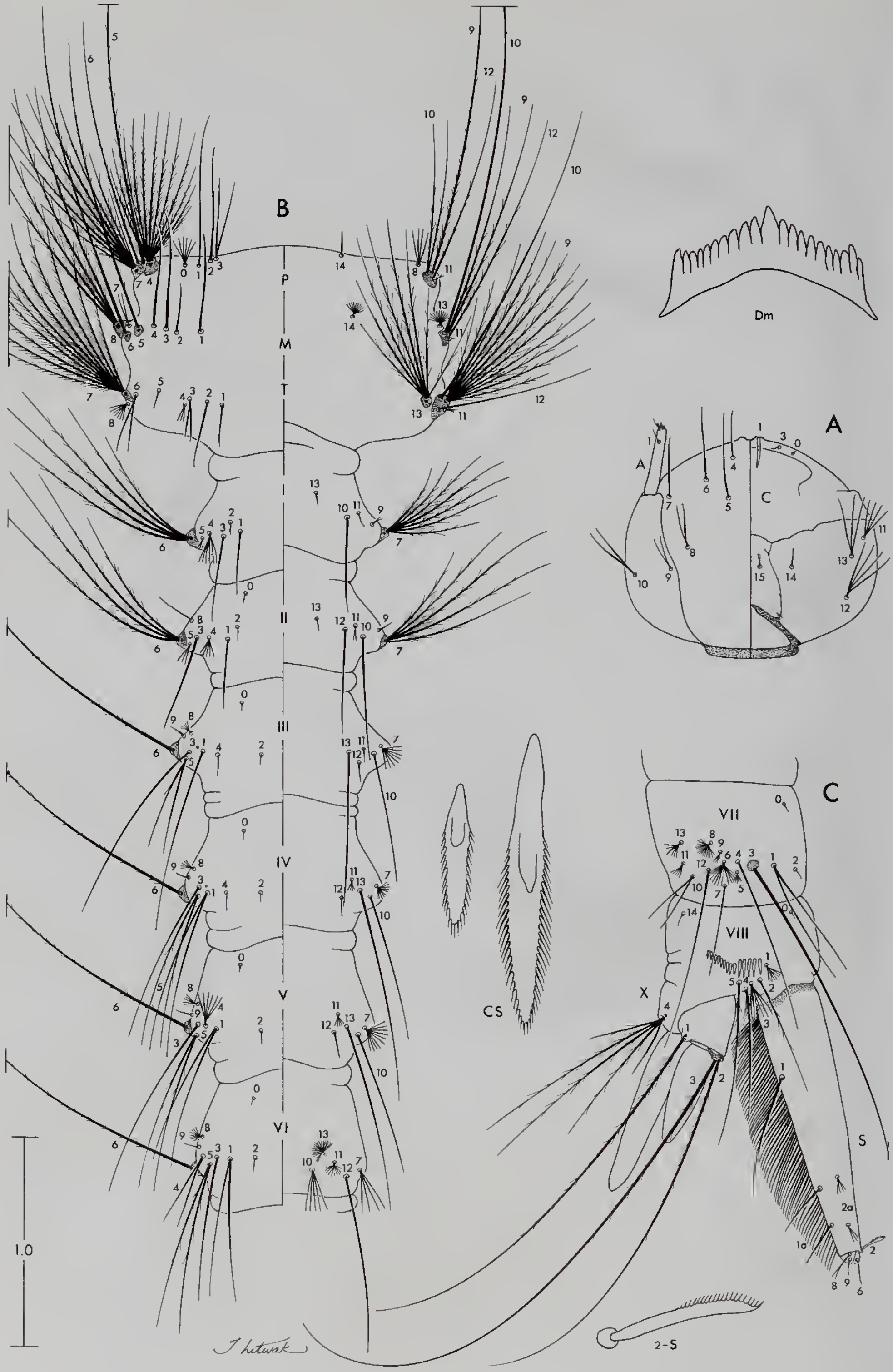

Fig. 19. Fourth-instar larva of *Onirion regale*. A, Head, dorsal and ventral aspects of left side; B, thorax and abdominal segments I–VI, dorsal and ventral aspects of left side; C, abdominal segments VII–X, left side. Scale in mm.

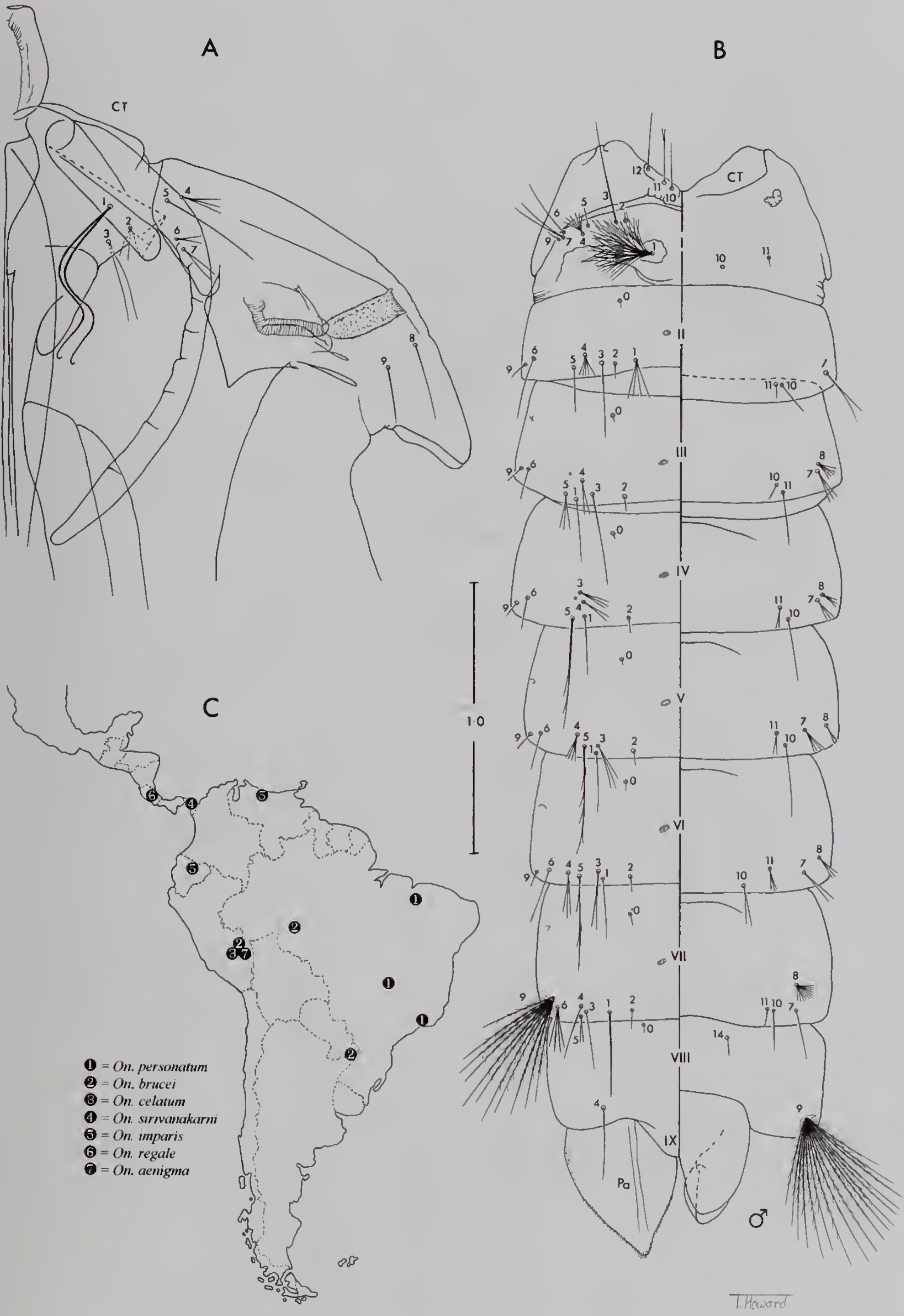

Fig. 20. A,B, Pupa of *Onirion aenigma*: (A) left side of cephalothorax, dorsal to right; (B) dorsal (left) and ventral (right) aspects of metathorax and abdomen. C, Map of Central and South America showing the areas where species of *Onirion* are known to occur. Scale in mm.

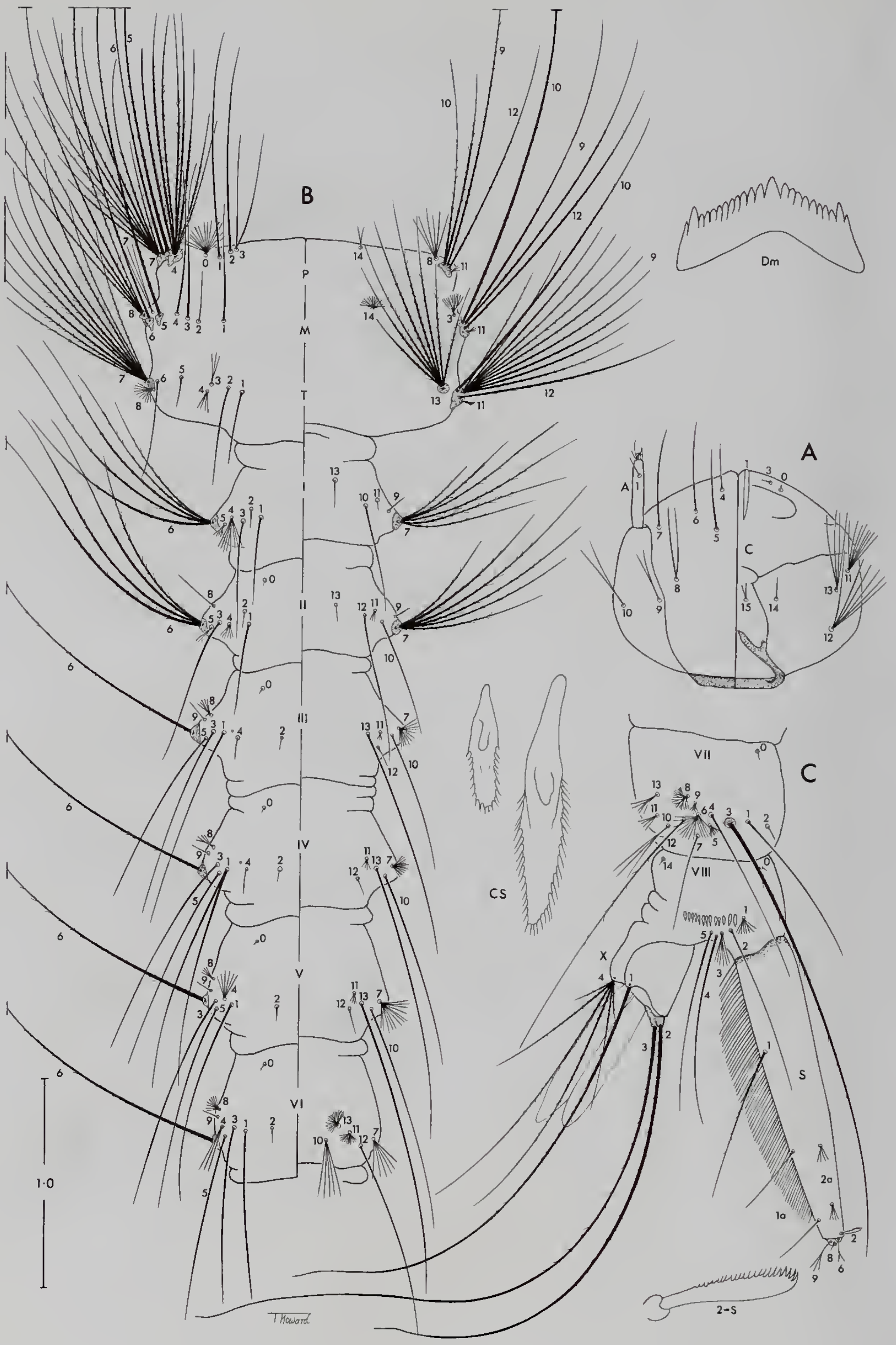

Fig. 21. Fourth-instar larva of *Onirion aenigma*, reconstructed from exuviae. A, Head, dorsal and ventral aspects of left side; B, thorax and abdominal segments I–VI, dorsal and ventral aspects of left side; C, abdominal segments VII–X, left side. Scale in mm.

Table 1. Lengths (in mm) of selected structures measured in adults of the species of *Onirion*. Means in parentheses.

Structure	*personatum*	*brucei*	*celatum*	*sirivanakarni*	*imparis*	*regale*	*aenigma*
Antenna	2.10–2.24(2.17)	1.75–2.21(1.97)	1.93–2.10(2.04)	1.75–2.28(2.10)	1.82–2.10(1.97)	2.10–2.17(2.12)	1.75–2.10(1.89)
Proboscis	2.10–2.20(2.14)	1.75–2.24(1.96)	2.03–2.14(2.09)	1.82–2.24(2.01)	1.96–2.17(2.11)	2.03–2.21(2.15)	1.93–2.10(2.01)
Maxillary palpus	0.35–0.42(0.40)	0.28–0.42(0.35)	0.28–0.42(0.36)	0.32–0.46(0.38)	0.28–0.35(0.32)	0.32–0.42(0.39)	0.28–0.39(0.32)
Wing	3.92–4.27(4.11)	3.26–4.52(3.90)	3.61–4.27(3.98)	3.43–4.55(3.87)	3.71–3.92(3.83)	3.68–4.27(4.04)	3.50–4.13(3.76)
Forefemur	2.87–3.15(3.00)	2.28–3.15(2.73)	2.80–2.94(2.86)	2.31–3.08(2.83)	2.73–2.94(2.84)	2.98–3.15(3.07)	2.63–2.87(2.75)
Midfemur	2.80–3.05(2.92)	2.10–2.96(2.59)	2.70–2.80(2.74)	2.24–2.98(2.73)	2.56–2.80(2.72)	2.80–2.98(2.91)	2.63–2.80(2.73)
Hindfemur	2.38–2.52(2.45)	1.75–2.63(2.15)	2.24–2.35(2.30)	1.89–2.49(2.29)	2.24–2.38(2.33)	2.35–2.45(2.41)	2.14–2.38(2.26)
Hindtibia	2.26–2.35(2.30)	1.75–2.45(2.07)	2.10–2.28(2.22)	1.86–2.35(2.21)	2.10–2.28(2.21)	2.24–2.45(2.32)	2.10–2.31(2.17)
Hindtarsomere 1	2.52–2.63(2.56)	1.68–2.80(2.29)	2.45–2.63(2.56)	2.10–2.66(2.45)	2.28–2.59(2.46)	2.31–2.56(2.43)	2.28–2.45(2.35)
Forefemur/proboscis	1.32–1.45(1.40)	1.30–1.51(1.39)	1.33–1.38(1.37)	1.27–1.55(1.41)	1.31–1.39(1.35)	1.41–1.47(1.43)	1.36–1.39(1.37)

Table 2. Numbers of various setae observed in adults of the species of *Onirion*. Modes in parentheses.

Setae	*personatum*	*brucei*	*celatum*	*sirivanakarni*	*imparis*	*regale*	*aenigma*
Labial basal	♀ 6–8(7) ♂ 9–11(10)	♀ 6–8(8) ♂ 8–15(10)	♀ 5–7(6) ♂ 20–24	♀ 5–7(6) ♂ 13–17	♀ – ♂ 9,10(10)	♀ 5–7 ♂ 20,22	♀ – ♂ 8–12
Antedorsocentral	6–10(7)	5–14(7)	6–8(7)	5–8(7)	6–9(6)	7–11(8)	6–9(7)
Supraalar	18–32	20–34	27–38	22–32	27–35	29–42	20–25
Prescutellar (both sides)	♀ 2,3(2) ♂ 3–5(3)	♀ 0,2(2) ♂ 1,2(2)	♀ 1,2(2) ♂ 2–5	♀ 1,2(1) ♂ –	♀ 2 ♂ 2,3(3)	♀ 2,3(2) ♂ 1–4(3)	♀ – ♂ 1,2
Scutellar – lateral lobe	9–12(10)	7–12(8)	8–11(10)	8–11(8)	9–11(9)	8–14(9)	9–12(9)
Scutellar – mesal lobe	8–10(9)	6–9(6)	7–11(10)	8–12(9)	5–9(8)	6–10(8)	6,7
Mesopostnotal	6–8(8)	6–8(7)	8–10(8)	7–11(8)	6–9(8)	7–9(9)	6–10
Antepronotal	12–18(12)	9–23(14)	12–23(16)	13–21(16)	14–20(15)	12–19(17)	14–18(16)
Prespiracular	3,4(3)	2–8(3)	4–6(4)	4–6(6)	4–6(6)	4–8(7)	3–6
Upper proepisternal	5–7(5)	3–8(3)	6–8(6)	3–5(5)	3–5(5)	2–5(3)	4,5(4)
Lower mesokatepisternal	6–10(7)	4–8(6)	6–8(8)	4–6(6)	5–8(6)	5–7(6)	7–9(7)
Prealar	3–6(5)	4,5(4)	3–5(4)	3–5(5)	2–4(4)	4–6(5)	4
Upper mesepimeral	11–14(12)	8–10(9)	9–13(12)	9–13(12)	10–14(10)	9–13(11)	9–14
Upper calypter	1–3(2)	1–3(1)	1–3(2)	1–3(2)	2	1–3(2)	2

Table 3. Numbers of branches for setae of pupae of *Onirion personatum*. Range (mode) based on five specimens (10 setae) from Brazil.

	Cephalothorax	Abdominal segments									Paddle
Seta	CT	I	II	III	IV	V	VI	VII	VIII	IX	P
0	–	–	1	1	1	1	1	1	1	–	–
1	2	83+	1–3(2)	1	1,2(1)	1,2(1)	1,2(1)	1,2(1)	–	–	–
2	1–3(3)	1	1	1	1	1	1	1	–	–	–
3	3–5(3)	1	1	1	1–3(2)	1–3(2)	2,3(2)	1,2(1)	–	–	–
4	3	3–9(4)	4–6(4)	1,2(2)	1–5(4)	3–6(5)	2–4(3)	1	1,2(1)	–	–
5	1,2(1)	1,2(1)	1	2–4(4)	1,2(1)	1,2(1)	1,2(1)	2–5(3)	–	–	–
6	1–4(2)	1,2(1)	1	1	1,2(1)	1	1	2–8(5)	–	–	–
7	1–3(2)	1,2(1)	2,3(2)	2–4(2)	2–4(2)	3–8(3)	1,2(2)	1	–	–	–
8	1	–	–	2–11(5)	1,2(1)	1,2(2)	1–4(2)	6–8(6)	–	–	–
9	1	1,2(1)	1	1	1	1	1	8–13(11)	11–16(15)	–	–
10	1,2(1)	–	1,2(1)	1,2(1)	1,2(1)	1	1,2(1)	1	–	–	–
11	1–6(3)	1	0,1(1)*	1,2(1)	1,2(1)	1–4(1)	2–5(3)	1,2(1)	–	–	–
12	1,2(1)	–	–	–	–	–	–	–	–	–	–
13	–	–	–	–	–	–	–	–	–	–	–
14	–	–	–	–	–	–	–	–	1	–	–

* Sometimes absent or alveolus without seta present.

Table 4. Numbers of branches for setae of fourth-instar larvae of *Onirion personatum*. Range (mode) based on five specimens (10 setae) from Brazil.

	Head	Thorax			Abdominal segments								
Seta	C	P	M	T	I	II	III	IV	V	VI	VII	VIII	X
0	1	13–23	–	–	–	1	1	1	1	1	1	1	–
1	1	1	1	1	1	1,2(1)	1	2	2	2,3(3)	2,3(3)	10–15(10)	1
2	–	1	1	1	1	1	1	1	1	1	1	1	1
3	1	1,2(2)	1	2,3(3)	1	1	1	1	1	1	1	5–10(8)	1
4	1	6–8(6)	1	4–7(4)	4–6(5)	4–8(4)	1	1	4–6(5)	1–3(2)	1	1	3–5(4)
5	1	1	1	1	3,4(4)	2–4(2)	2	2	2	2	5–10(6)	1	–
6	1	1	1	1,2(1)	4–7(5)	3–8(4)	1	1	1	1	12–18(12)	–	–
7	1	7–10(8)	1–4(1)	8–11(9)	4–8(5)	3–6(4)	10–13(13)	10–16(14)	9–13(10)	5–8(5)	1,2(1)	–	–
8	1,2(2)	4–6(4)	3–5(3)	9–12(10)	–	1	3–5(5)	3,4(4)	4–7(5)	9–11(10)	20–34	1-S,	1
9	2–4(2)	1	2	9–12(11)	1	1	1	1	1,2(1)	1,2(1)	8–10(9)	1a-S,	1,2(1)
10	2–4(2)	1,2(2)	1	1	1	1	1	1	1	3–6(5)	2–5(3)	2a-S,	3–9(5,6)
11	4–9(7)	3–5(4)	3–5(4)	4–7(6)	1	3–5(4)	4,5(5)	4,5(4)	4–6(5)	7–12(10)	5,6(5)	–	–
12	3–5(4)	1	1	1	–	1	1	1	1	1(1)	1	–	–
13	2–4(4)	–	11–14(13)	5–9(7)	1	1	1	1	1	~30	5–9(6)	–	–
14	1	1,2(2)	~20	–	–	–	–	–	–	–	–	1	–
15	2–5(3)	–	–	–	–	–	–	–	–	–	–	–	–

Table 5. Numbers of branches for setae of pupae of *Onirion brucei*. Range (mode) based on five specimens (10 setae) from Argentina and Peru.

	Cephalothorax	Abdominal segments									Paddle
Seta	CT	I	II	III	IV	V	VI	VII	VIII	IX	P
0	–	–	1	1	1	1	1	1	1	–	–
1	2	74+	1–4(3)	1,2(1)	1	1,2(1)	1–3(1)	1	–	–	–
2	2–5(4)	1	1	1	1	1	1	1	–	–	–
3	1,2(2)	1	1	1,2(1)	1–4(2)	1–4(2)	1–3(2)	1–3(2)	–	–	–
4	1–3(2)	3–7(5)	4–6(5)	1–3(2)	2–6(5)	3–5(4)	2–4(2)	1	1,2(1)	–	–
5	1,2(1)	1,2(1)	1	1–4(3)	1,2(1)	1	1–3(1)	1–4(3)	–	–	–
6	1–4(2)	1,2(1)	1	1,2(1)	1,2(1)	1,2(1)	1,2(1)	3–10(3)	–	–	–
7	1,2(2)	1,2(1)	1,2(2)	1–3(3)	1–4(3)	3–5(4)	1–4(1)	1	–	–	–
8	1,2(1)	–	–	1–6(3)	1–3(1)	1–4(2)	1–3(3)	3–7(6)	–	–	–
9	1,2(1)	1,2(1)	1	1	1	1	1	8–16(8)	14–18(15)	–	–
10	1,2(1)	–	1	1	1	1	1–3(2)	1,2(1)	–	–	–
11	1,2(1)	0,1(0)	0,1(1)*	1,2(1)	1,2(1)	2,3(2)	1–4(3)	1,2(1)	–	–	–
12	1	–	–	–	–	–	–	–	–	–	–
13	–	–	–	–	–	–	–	–	–	–	–
14	–	–	–	–	–	–	–	–	1	–	–

* Sometimes alveolus present without seta.

Table 6. Numbers of branches for setae of fourth-instar larvae of *Onirion brucei*. Range (mode) based on eight specimens (16 setae) from Argentina and Peru.

	Head	Thorax			Abdominal segments								
Seta	C	P	M	T	I	II	III	IV	V	VI	VII	VIII	X
0	1	10–15(11)	–	–	–	1	1	1	1	1	1	1	–
1	1	1	1	1	1	1	1	2	2	1–3(2)	2,3(2)	8–13(11)	1
2	–	1	1	1	1	1	1	1	1	1	1	1	1
3	1	1–3(2)	1	1–3(3)	1	1	1	1	1	1	1	4–8(6)	1
4	1	6–9(7)	1,2(1)	4–7(5)	4–7(5)	3–6(5)	1–3(1)	1,2(1)	4–8(6)	2,3(3)	1	1,2(1)	3,4(4)
5	1,2(1)	1	1	1	3–5(4)	2–4(2)	1	1	1	1	4–6(5)	1	–
6	1	1	1	1,2(1)	5–8(5)	5	1	1	1	1	11–19(13)	–	–
7	1	6–11(8)	1–5(2)	8–11(9)	6–10(6)	3–8(4)	8–15(10)	7–11(10)	6–12(9)	4–6(6)	1	–	–
8	1,2(2)	4–8(5)	3–5(4)	10–13(10)	–	1	1–4(3)	2–4(4)	1–5(3)	5–10(8)	15–28(20)	1-S,	1
9	1–3(2)	1	2,3(2)	9–14(10)	1,2(1)	1	1	1	1	1	4–10(6)	1a-S,	1,2(1)
10	1–4(3)	1,2(2)	1	1	1	1	1	1	1	5–7(5)	2,3(3)	2a-S,	2–7(3)
11	5–9(6)	2,3(2)	1–4(1)	4–6(5)	1	2–4(3)	2–5(3)	2–7(5)	3–6(5)	9–15(10)	4–10(8)	–	–
12	4–6(5)	1	1	1	–	1	1	1	1	1	1	–	–
13	2–5(4)	–	13–18(16)	7–9(8)	1	1	1	1	1	~25	4–6(5)	–	–
14	1	1–3(2)	~18	–	–	–	–	–	–	–	–	1	–
15	1–4(2)	–	–	–	–	–	–	–	–	–	–	–	–

Table 7. Numbers of branches for setae of pupae of *Onirion celatum*. Range (mode) based on five specimens (10 setae) from Peru.

	Cephalothorax	Abdominal segments									Paddle
Seta	CT	I	II	III	IV	V	VI	VII	VIII	IX	P
0	–	–	1	1	1	1	1	1	1	–	–
1	2	75+	1–8(5)	1,2(1)	1–3(1)	1,2(1)	1,2(1)	1	–	–	–
2	3–5(4)	1	1	1	1	1	1	1	–	–	–
3	1,2(2)	1	1	1,2(1)	2,3(2)	1–3(2)	1–3(3)	1,2(1)	–	–	–
4	1–4(2)	4–8(5)	4–7(6)	2,3(2)	2–6(5)	3–6(3)	1–3(2)	1	1,2(1)	–	–
5	1–3(1)	1,2(1)	1,2(1)	2,3(2)	1,2(1)	1–3(2)	1–4(2)	1–4(2)	–	–	–
6	1,2(1)	1	1	1	1	1	1	3–8(5)	–	–	–
7	1–3(2)	1,2(1)	1,2(2)	1–4(2)	2–4(4)	3–7(5)	1,2(1)	1	–	–	–
8	1,2(1)	–	–	2–7(5)	1–3(2)	1–3(2)	1–9(3)	3–10(6)	–	–	–
9	1	1	1	1	1	1	1	10–14(11)	13–22(16)	–	–
10	2,3(2)	–	1,2(1)	1	1	1	1	1	–	–	–
11	1–3(1)	1	1–3(1)	1,2(1)	1–3(1)	1,2(2)	3,4(3)	1–3(2)	–	–	–
12	1,2(1)	–	–	–	–	–	–	–	–	–	–
13	–	–	–	–	–	–	–	–	–	–	–
14	–	–	–	–	–	–	–	–	1	–	–

Table 8. Numbers of branches for setae of fourth-instar larvae of *Onirion celatum*. Range (mode) based on five specimens (10 setae) from Peru.

	Head	Thorax			Abdominal segments								
Seta	C	P	M	T	I	II	III	IV	V	VI	VII	VIII	X
0	1	10–13(11)	–	–	–	1	1	1	1	1	1	1	–
1	1	1	1	1	1	1	1	2	2	1,2(1)	1,2(2)	6–11(8)	1
2	–	1	1	1		1	1	1	1	1	1	1	1 1
3	1	2,3(2)	1,2(1)	1–5(2)	1	1	1	1	1	1	1	5–7(6)	1
4	1	8–10(10)	1	4–6(4)	5–7(6)	4–7(5)	1	1	5–7(6)	2,3(2)	1	1	4–6(5)
5	1	1	1	1	3,4(4)	2,3(2)	1	1,2(1)	1	1	5–8(6)	1	–
6	1,2(1)	1	1	1,2(1)	5–7(6)	5	1	1	1	1	9–13(13)	–	–
7	1	7–11(8)	1,2(2)	11–13(12)	6,7(7)	5–7(5)	10–13(12)	8–11(10)	10–13(12)	3–6(4)	1	–	–
8	2	4–7(6)	4,5(5)	10	–	1	2–5(3)	4–8(4)	4–7(4)	7–10(8)	15–20	1-S,	1
9	1,2(2)	1	2	10–15	1–4(2)	1	1	1	1	1,2(1)	6–13	1a-S,	1
10	1–3(2)	2	1	1	1	1	1	1	1	5–8(5)	2,3(2)	2a-S,	3–8(4)
11	5–9(6)	2–4(3)	2–4(2)	4–6(4)	1	2–5(4)	3,4(3)	4,5(4)	2–5(4)	10–13(10)	6–11(10)	–	–
12	3–5(3)	1	1	1	–	1	1	1	1–3(1)	1	1	–	–
13	3–5(3)	–	15–18(16)	8–10(8)	1	1	1	1	1	25–39	5,6(6)	–	–
14	1	1–3(2)	~20	–	–	–	–	–	–	–	–	1	–
15	2,3(2)	–	–	–	–	–	–	–	–	–	–	–	–

Table 9. Numbers of branches for setae of pupae of *Onirion imparis*. Range (mode) based on one specimen (two setae) from Venezuela.

	Cephalothorax	Abdominal segments									Paddle
Seta	CT	I	II	III	IV	V	VI	VII	VIII	IX	P
0	–	–	1/1	1/1	1/1	1/1	1/1	1/1	1/1	–	–
1	2/2	71+	1/2	1/1	1/–	–/1	1/1	1/1	–	–	–
2	2/3	2/5	1/1	1/1	1/1	1/1	1/1	1/1	–	–	–
3	2/2	1/1	1/1	1/2	3/3	1/1	3/2	1/1	–	–	–
4	3/3	6/4	3/4	1/1	1/1	4/4	2/3	1/1	1/1	–	–
5	–/1	1/1	1/1	3/2	1/1	1/1	1/1	2/2	–	–	–
6	1/2	1/1	1/1	1/1	1/–	–/–	1/1	5/4	–	–	–
7	2/2	1/1	2/2	1/2	1/2	4/3	2/2	1/1	–	–	–
8	1/2	–	–	3/3	1/1	1/1	2/1	2/6	–	–	–
9	1/1	1/1	1/1	1/1	1/1	1/1	1/1	11/9	14/13	–	–
10	1/1	–	1/1	1/1	1/1	1/1	1/1	1/1	–	–	–
11	1/1	–/–	*	1/1	1/1	1/1	2/3	1/1	–	–	–
12	1/–	–	–	–	–	–	–	–	–	–	–
13	–	–	–	–	–	–	–	–	–	–	–
14	–	–	–	–	–	–	–	–	1/1	–	–

* Alveolus present without seta.

Table 10. Numbers of branches for setae of fourth-instar larvae of *Onirion imparis*. Range (mode) based on two specimens (four setae) from Venezuela.

	Head	Thorax			Abdominal segments								
Seta	C	P	M	T	I	II	III	IV	V	VI	VII	VIII	X
0	1	10–14	–	–	–	1	1	1	1	1	1	1	–
1	1	1	1	1	1	1	1	2	2	2	2	10–13+	1
2	–	1	1,2(1)	1	1	1	1	1	1	1	1	1	1
3	1	2	1	3,4)3)	1	1	1	1	1	1	1	7,8(7)	1
4	1	7–9(9)	1	4–5	4–7	4–8	1	1	4–6	2,3(2)	1	1	4–6(5)
5	1	1	1	1	3,5	2,3(3)	1	1,2	1	1	3–9	1	–
6	1	1	1	1,2	5–7(6)	4	1	1	1	1	12–16	–	–
7	1	5–9(9)	2,5	9,10(9)	4–6(5)	3,4(4)	12–14	10+	9–13	6–8(8)	1	–	–
8	2,3(2)	6,7	4,5	10+	–	1	5,6	5–7	4–6(4)	10–15	30–35+	1-S,	1
9	1,2	1	2	10–13(11)	1	1	1	1	1	1,2	6–9	1a-S,	1
10	3,4(3)	2	1	1	1	1	1	1	1	5–6	3	2a-S,	3,4(4)
11	5–8	3	2	4,5(5)	1	2,3(3)	3,4(4)	2	3	10–15	7	–	–
12	5,6(5)	1	1	1	–	1	1	1	1	1	1	–	–
13	3–5(5)	–	14+	7,8	1	1	1	1	1	30+	8,9(9)	–	–
14	1,2	2,3	15+	–	–	–	–	–	–	–	–	1	–
15	2,3	–	–	–	–	–	–	–	–	–	–	–	–

Table 11. Numbers of branches for setae of fourth-instar larvae of *Onirion regale*. Range (mode) based on four specimens (eight setae) from Costa Rica.

	Head	Thorax			Abdominal segments								
Seta	C	P	M	T	I	II	III	IV	V	VI	VII	VIII	X
0	1	7–11(10)	–	–	–	1	1	1	1	1	1	1	–
1	1	1	1	1	1	1	1	2	2	2	2	4–10(6)	1
2	–	1	1	1	1	1	1	1	1	1	1,2(1)	1	1
3	1	2	1	2.3(3)	1	1	1	1	1	1	1	3–6(6)	1
4	1	10–12(11)	1	4,5(5)	4–7(5)	4–8	1	1	6,7(6)	2	1	1	5–10(5)
5	1	1	1	1	2–4(2)	1–4(3)	1,2(2)	2	2	2	4–6(5)	1	–
6	1	1	1	2–6(2)	5,6(6)	3–5(4)	?	?	?	?	9–16(12)	–	–
7	1	8–12(11)	2,3(2)	11–13(11)	6,7(7)	3–6(4)	7–14(11)	8–14(13)	7–11(9)	4–6(5)	1	–	–
8	1,2	3,4(4)	4,5(4)	6–11(9)	–	1	3–5(5)	4–6(4)	4,5(5)	6–11(9)	14–19(16)	1-S,	1
9	2,3(3)	1	2	11–14(11)	1,2(1)	1	1	1	1	1	3–5(4)	1a-S,	1–3(2)
10	3,4(3)	2	1	1	1	1	1	1	1	5,6(6)	1,2(2)	2a-S,	2–6(5)
11	3–5(4)	2,3(2)	2,3	5,6(5)	1	1–3(3)	2–4(4)	3,4	3–5(4)	7–12(9)	4,5(4)	–	–
12	4	1	1	1	–	1	1	1	1	1	1	–	–
13	2,3(3)	–	10–13(11)	8–10(8)	1	1	1	1	1	21–31(26)	6–8(7)	–	–
14	1	1–3(1)	7–13	–	–	–	–	–	–	–	–	1	–
15	2	–	–	–	–	–	–	–	–	–	–	–	–

Table 12. Numbers of branches for setae of pupae of *Onirion aenigma*. Range (mode) based on three specimens (six setae) from Peru.

	Cephalothorax	Abdominal segments									Paddle
Seta	CT	I	II	III	IV	V	VI	VII	VIII	IX	P
0	–	–	1	1	1	1	1	1	1	–	–
1	2	85+	3,4(4)	1,2(1)	1	1	1,2(1)	1	–	–	–
2	2–4(4)	1,2(1)	1	1	1	1	1	1	–	–	–
3	1,2(2)	1	1	1,2(1)	1–3(2)	1–4(3)	2,3(2)	1,2(1)	–	–	–
4	1–3(2)	5–7(7)	4–6(5)	2,3(2)	3–6(4)	3–6(4)	1–3(3)	1	1	–	–
5	1,2(1)	1,2(1)	1	2–4(2)	1–3(1)	1–3(1)	1–3(1)	2–5(2)	–	–	–
6	1,2(2)	1	1	1	1	1,2(1)	1	1–6(3)	–	–	–
7	2,3(2)	1–3(2)	1–3(2)	2,3(3)	2–5(3)	3–5(4)	1–3(1)	1	–	–	–
8	1	–	–	4–7(5)	1–5(2)	1,2(2)	2–4(3)	5–11(11)	–	–	–
9	1	1	1	1	1	1	1	9–13(11)	15–19(17)	–	–
10	1	0,1*	1,2(1)	1	1	1,2(1)	1,2	1	–	–	–
11	2,3(2)	0,1	0,1(1)*	1,2(1)	1,2(2)	1–3(2)	3–5(3)	1	–	–	–
12	1	–	–	–	–	–	–	–	–	–	–
13	–	–	–	–	–	–	–	–	–	–	–
14	–	–	–	–	–	–	–	–	1	–	–

* Sometimes alveolus present without seta.

Table 13. Numbers of branches for setae of fourth-instar larvae of *Onirion aenigma*. Range (mode) based on three specimens (six setae) from Peru.

	Head	Thorax			Abdominal segments								
Seta	C	P	M	T	I	II	III	IV	V	VI	VII	VIII	X
0	1	13–18(14)	–	–	–	1	1	1	1	1	1	1	–
1	1	1	1	1	1	1	1	2	1	1	1	7–12	1
2	–	1	1	1	1	1	1	1	1	1	1	1	1
3	1	2	1	2–4(3)	1	1	1	1	1	1	1	4–6(6)	1
4	1	6–10(8)	1	4,5	5–8(8)	4–8(6)	1	1	4–10(8)	2–4(3)	1	1,2(1)	4–7(7)
5	1	1	1	1	2–4(3)	1–3(2)	1	1	1	1	4–6(6)	1	–
6	1	1	1	1,2	4–7(5)	3,4	1	?	?	1	10–19	–	–
7	1	9–12	2,3(3)	9–11(10)	6–9(6)	4–7(6)	12–20(12)	8–13(12)	10–15(12)	5,6(6)	1	–	–
8	1,2(2)	5–8(7)	5	10–17(14)	–	1	4,5(5)	2–4(4)	3–5	7–10(9)	22–29	1-S,	1
9	2,3(2)	1	1,2	10–13	1	1	1	1	1,2(1)	1	3–9	1a-S,	1,2(1)
10	2,3(2)	2	?	1	1	1	1	1	1	5–6(5)	2–4(3)	2a-S,	3–6(4)
11	6–8(8)	2–4(3)	2–5(4)	3–5(4)	1	3,4(3)	3,4(3)	2–4(3)	2–5(4)	7–16(10)	4,5(4)	–	–
12	4–7(6)	1	?	1	–	1	1	1	1	1	1	–	–
13	4	–	11–20(14)	7,8(8)	1	1	1	1	1	36–48	4–8(5)	–	–
14	1	2	15–19(19)	–	–	–	–	–	–	–	–	1	–
15	2,3	–	–	–	–	–	–	–	–	–	–	–	–

APPENDIX 1

Anatomical characters used in the cladistic analysis. See Harbach & Kitching (1998) for discussion and illustrations of the characters. See Appendix 2 for character state(s) observed in the analysed taxa.

Larvae (fourth-instars)

1. *Hypostomal suture*: (0) short to absent, not reaching posterior tentorial pit; (1) complete to posterior tentorial pit.
2. *Occipital foramen*: (0) circular to oval; (1) transverse and slit-like.
3. *Maxillary palpus*: (0) appended to maxillary body; (1) fused with maxillary body.
4. *Hypostomal sclerite*: (0) part of lateralia; (1) narrowly attached to lateralia; (2) detached from lateralia.
5. *Hypostomal sclerite and maxillary palpus*: (0) separate; (1) fused.
6. *Hypostomal sclerite and maxillary body*: (0) separate; (1) fused.
7. *Apical process of maxilla*: (0) absent; (1) present.
8. *Maxillary brush*: (0) composed of independent spicules; (1) represented by a flexible bundle of coalesced spicules; (2) represented by a solid claw-like structure without evidence of individual elements.
9. *Seta 2-C*: (0) absent; (1) present.
10. *Seta 3-C*: (0) absent; (1) present, on oral surface of head; (2) present, on adoral surface of head.
11. *Seta 13-P*: (0) absent; (1) present.
12. *Seta 8-M*: (0) absent; (1) present.
13. *Seta 1 on some or all of abdominal segments I–VII*: (0) with flattened leaf-like branches (palmate); (1) with normal stem-like branches.
14. *Setae 6,7-I,II*: (0) single main stem with numerous regularly arranged branches arising on either side (plumose); (1) one or more main stems without plumose branching.
15. *Seta 12-I*: (0) absent; (1) present.
16. *Seta 5-VIII*: (0) removed from seta 4, well below level of dorsal margin of segment X; (1) close to seta 4, usually near or above level of dorsal margin of segment X.
17. *Comb*: (0) absent; (1) present.
18. *Comb plate*: (0) absent or weakly developed; (1) present, well developed.
19. *Siphon* (degree of development): (0) absent; (1) lobe with a narrow posterior band of sclerotized cuticle; (2) short tube with separate anterior and posterior sclerites; (3) elongate fully sclerotized tube.
20. *Seta 1-S*: (0) inserted at base of siphon; (1) inserted beyond base of siphon.
21. *Pecten*: (0) absent; (1) composed of spines; (2) composed of filaments.
22. *Accessory setae of siphon* (*other than 1,2-S*): (0) absent; (1) present.
23. *Saddle*: (0) absent; (1) incomplete; (2) complete, forming a ring around segment X.
24. *Pairs of seta 4-X*: (0) absent; (1) one pair; (2) 2 pairs; (3) 4 pairs; (4) usually ≥5 pairs.

Pupae

25. *Dorsal apotome*: (0) evenly sclerotized, appearing as a single sclerite; (1) weakly sclerotized medially, appearing as two sclerites joined by membrane.
26. *Trumpet*: (0) supporting tubercle absent; (1) present.
27. *Tracheoid area of trumpet*: (0) absent; (1) present.
28. *Seta 1-CT* (degree of development): (0) absent; (1) normal, similar in development to setae 2,3-CT; (2) very strongly developed, considerably larger than setae 2,3-CT.
29. *Seta 14-III–VII*: (0) absent; (1) present.
30. *Seta 9-IV–VII*: (0) at or very near caudolateral angle of tergum; (1) removed from caudolateral angle of tergum.
31. *Seta 0-VIII*: (0) inserted on anterior area of tergum; (1) inserted at mid-length or on posterior area of tergum.
32. *Seta 9-VIII*: (0) ventral in insertion; (1) dorsal in insertion; (2) inserted midway between dorsal and ventral surfaces.
33. *Seta 14-VIII*: (0) absent; (1) approximated; (2) widely separated.
34. *Seta 1-IX*: (0) absent; (1) present.
35. *Seta 1-XI*: (0) absent; (1) present.
36. *Paddle seta(e)*: (0) absent; (1) present.

Adults (both sexes except where otherwise indicated)

37. *Erect scales of head*: (0) absent; (1) few and restricted to occiput; (2) numerous and not restricted to occiput.
38. *Interocular space* (principally females): (0) constricted, without scales/setae extending to postfrontal sutures; (1) broader with scales/setae extending to postfrontal sutures.
39. *Interantennal ridge* (females): (0) complete, with very short or conjoined dorsal arms reaching postfrontal sutures and engulfing frontal pit (when evident); (1) incomplete in dorsal area of postfrons, with frontal pit reinforced by cuticular ring associated with postfrontal sutures; (2) entirely absent from postfrons, with discrete frontal pit usually removed from postfrontal sutures.
40. *Interantennal ridge* (males): (0) complete in postfrons; (1) incomplete (absent) in postfrons.
41. *Basal microsetae of antennal pedicel*: (0) absent; (1) present.
42. *Apical flagellomeres* (males): (0) one or both (usually) of two apical flagellomeres disproportionately long compared with the other flagellomeres; (1) these flagellomeres not disproportionately long in comparison with the others.
43. *Maxillary palpomeres* (females): (0) five fully developed; (1) four, fifth vestigial or absent; (2) three, fourth vestigial or absent; (3) two, third vestigial if present; (4) one.
44. *Maxillary palpomeres* (males): (0) five; (1) four; (2) three, fourth vestigial or absent; (3) two, third vestigial or absent; (4) one.
45. *Mouthparts*: (0) short, not developed into a proboscis; (1) long, developed into a proboscis.
46. *Labellum*: (0) comprising two separate sclerites; (1) comprising partially (ventrally) fused proximal and distal sclerites; (2) comprising a single sclerite.
47. *Proximal sclerite of labellum*: (0) absent or unrecognisably fused with distal sclerite; (1) short, similar in size to distal sclerite; (2) elongate, distinctly longer than distal sclerite.
48. *Labellar scaling*: (0) absent; (1) present.
49. *Antepronota*: (0) large and approximated; (1) smaller (usually) and more widely separated.
50. *Acrostichal setae*: (0) absent; (1) present.
51. *Dorsocentral setae*: (0) absent; (1) present.
52. *Scutellum*: (0) evenly rounded; (1) trilobed.
53. *Mesopostnotal setae and/or scales*: (0) absent; (1) present.
54. *Paratergite*: (0) bare; (1) with scales or setae.
55. *Postpronotal setae*: (0) absent; (1) present.
56. *Prespiracular setae*: (0) absent; (1) present.
57. *Postspiracular setae*: (0) absent; (1) present.
58. *Prealar setae*: (0) absent; (1) present.
59. *Upper mesokatepisternal setae*: (0) absent; (1) present.
60. *Lower mesepimeral seta(e)*: (0) absent; (1) present.
61. *Metepisternal scales*: (0) absent; (1) present.
62. *Upper calypter*: (0) bare; (1) with one or more setae or hair-like scales.
63. *Vestiture of alula*: (0) absent; (1) present.
64. *Vein R_s with basal spur*: (0) absent; (1) present.
65. *Vein R_2*: (0) shorter than vein R_{2+3}; (1) equal or longer than vein R_{2+3}.
66. *Precubital furrow*: (0) absent; (1) present.
67. *Anal vein*: (0) ends before or at junction of mcu and CuA; (1) ends beyond junction of mcu and CuA.
68. *Microtrichia of wing membrane*: (0) minute, inconspicuous at low magnification; (1) distinct, clearly visible at low magnification.
69. *Tarsomere 1 of fore- and midlegs*: (0) shorter than tarsomeres 2–5 combined; (1) longer than tarsomeres 2–5 combined.
70. *Base of hindcoxa*: (0) well below dorsal margin of mesomeron; (1) more or less in line with or slightly above dorsal margin of mesomeron.
71. *Pulvilli*: (0) absent or rudimentary (inconspicuous); (1) distinctly developed (conspicuous).
72. *Spermathecal capsules* (females): (0) one; (1) three.
73. *Paraprocts* (males): (0) absent or only weakly developed; (1) strongly developed, apex without crown of spicules; (2) strongly developed, apex with crown of spicules.

APPENDIX 2

Data matrix for forty-three genera and seventy-three anatomical characters used in the cladistic analysis. *Phoniomyia* is included as a genus because it was a valid genus when Harbach & Kitching (1998) constructed the data matrix that was expanded to include *Onirion. Phoniomyia* was recently reduced to subgeneric status within *Wyeomyia* (Judd, 1998*b*), but was retained as a genus in the present analysis for convenience. This also applies to *Bironella*, which Sallum *et al.* (2000) synonymised with *Anopheles*, and *Verrallina*, *Ayurakitia* and *Ochlerotatus*, which Reinert (1999*b*, 2000*a* and 2000*b*, respectively) elevated from subgeneric status within *Aedes*. Navarro & Liria (2000) proposed the reduction of *Deinocerites* to subgeneric status within *Culex*, but we prefer to recognize it as a separate genus for the time being.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Corethrella	1	0	1	0	0	0	0	0	1	2	0	1	1	1	1	0	0	0	3	1	0	0	1	2	0
Eucorethra	1	0	1	0	0	0	0	0	1	2	0	1	1	1	1	0	0	0	2	?	0	0	0	4	0
Mochlonyx	1	0	1	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0	3	1	0	0	0	4	1
Nothodixa	0	0	0	2	0	0	0	0	1	2	0	1	1	1	0	0	0	0	0	?	1	0	1	0	0
Aedeomyia	1	1	0	?	?	?	0	0	0	2	0	1	1	1	1	0	1	1	3	1	0	0	2	4	1
Aedes	1	0	0	12	0	0	0	0	0	2	0	1	1	1	01	0	1	0	3	1	1	0	1	4	1
Anopheles	0	0	0	2	0	0	0	0	1	2	1	1	0	0	1	0	0	0	1	?	1	0	1	4	0
Armigeres	1	0	0	0	0	0	0	0	0	2	0	1	1	1	0	0	1	0	3	1	0	0	1	4	1
Bironella	0	0	0	2	0	0	0	0	1	2	1	1	0	0	1	0	0	0	1	?	1	0	1	4	0
Chagasia	1	0	0	2	0	0	0	0	1	2	1	1	0	0	1	0	0	0	1	?	1	0	1	4	0
Coquillettidia	1	0	0	1	0	0	0	0	0	2	0	1	1	1	1	1	1	0	3	1	0	0	2	4	1
Culex	1	0	0	1	0	0	0	0	0	2	0	1	1	1	1	0	1	0	3	1	1	1	2	4	1
Culiseta	1	0	0	12	0	0	0	0	0	2	0	1	1	1	1	0	1	0	3	01	1	0	2	4	1
Deinocerites	1	0	0	1	0	0	0	0	1	0	0	1	1	1	1	0	1	0	3	1	1	1	1	4	1
Eretmapodites	1	0	0	1	0	0	0	0	0	2	0	1	1	1	0	0	1	0	3	1	1	0	1	3	1
Ficalbia	1	0	0	0	0	0	0	0	0	2	0	1	1	1	1	1	1	0	3	0	1	0	2	4	1
Galindomyia	1	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	3	1	1	1	1	4	1
Haemagogus	1	0	0	1	0	0	0	0	0	2	0	1	1	1	1	0	1	0	3	1	1	0	1	4	1
Heizmannia	1	0	0	1	0	0	0	0	0	2	0	1	1	1	0	0	1	0	3	1	1	0	1	4	1
Hodgesia	1	0	0	2	1	0	0	0	0	2	0	1	1	1	1	1	1	0	3	0	1	0	2	3	1
Isostomyia	1	1	0	2	0	0	1	2	0	1	0	1	1	1	0	1	1	0	3	1	2	1	1	1	1
Johnbelkinia	0	0	1	2	0	1	1	1	0	1	0	1	1	1	0	1	1	0	3	1	0	1	1	1	1
Limatus	1	1	0	2	0	1	1	0	0	1	0	1	1	1	0	0	1	0	3	1	0	1	1	1	1
Malaya	1	1	1	2	0	1	1	0	0	1	0	1	1	1	0	1	1	0	3	1	1	1	1	1	1
Mansonia	1	0	0	1	0	0	0	0	0	2	0	1	1	1	1	1	1	0	3	1	0	0	2	4	1
Maorigoeldia	1	0	0	2	0	0	1	0	0	1	1	1	1	1	0	1	1	0	3	1	1	1	1	1	1
Mimomyia	0	0	0	2	01	0	0	0	0	2	0	1	1	1	1	1	1	0	3	1	01	0	12	23	1
Opifex	1	0	0	1	0	0	0	0	0	2	0	1	1	1	1	0	1	0	3	1	1	0	1	4	1
Onirion	1	0	0	2	0	1	1	0	0	1	0	1	1	1	0	1	1	0	3	1	2	1	1	1	1
Orthopodomyia	1	0	0	2	0	0	0	0	0	2	0	1	1	1	1	0	1	0	3	1	0	0	2	4	1
Phoniomyia	1	1	0	2	0	0	1	0	0	1	0	1	1	1	0	1	1	0	3	1	1	1	1	1	1
Psorophora	1	0	0	1	0	0	0	0	0	2	0	1	1	1	1	0	1	1	3	1	1	0	2	4	1
Runchomyia	1	1	0	2	0	0	1	1	0	1	0	1	1	1	0	1	1	0	3	1	2	1	1	1	1
Sabethes	1	1	1	2	0	1	1	0	0	1	0	1	1	1	0	1	1	0	3	1	2	1	1	1	1
Shannoniana	0	0	0	2	0	0	1	2	0	1	0	1	1	1	0	0	1	0	3	1	0	1	1	1	1
Topomyia	1	1	0	2	0	0	1	01	0	1	0	1	1	1	0	01	1	0	3	1	1	1	1	1	1
Toxorhynchites	0	0	0	0	0	0	0	0	0	2	0	1	1	1	1	0	0	0	3	1	0	0	2	4	1
Trichoprosopon	1	0	0	2	1	0	1	0	0	1	0	0	1	1	0	1	0	0	3	1	0	1	1	1	1
Tripteroides	01	0	0	2	1	0	1	02	0	1	1	01	1	1	0	01	1	0	3	1	1	1	1	1	1
Udaya	1	0	0	1	0	0	0	0	0	2	0	1	1	1	0	0	1	0	3	1	1	0	1	3	1
Uranotaenia	0	0	0	2	0	0	0	0	0	2	0	1	1	1	1	0	1	1	3	1	1	0	2	4	1
Wyeomyia	1	1	0	2	0	0	1	0	0	1	0	1	1	1	0	1	1	0	3	1	012	1	1	1	1
Zeugnomyia	1	0	0	1	0	0	0	0	0	2	0	1	1	1	1	0	1	0	3	1	1	0	1	3	1

Appendix 2, continued.

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Corethrella	1	0	0	1	1	0	0	0	1	0	1	0	1	1	0	1	1	0	0	0	2	0	0	1	1
Eucorethra	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	1
Mochlonyx	1	0	1	1	1	0	1	2	0	0	1	0	1	3	0	1	0	0	0	0	0	0	0	1	1
Nothodixa	1	1	1	1	1	0	0	2	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1
Aedeomyia	1	1	1	1	0	0	0	2	1	0	1	2	1	3	1	1	1	2	2	1	0	1	0	1	1
Aedes	0	1	1	1	1	0	0	2	0	0	1	12	01	1	1	1	0	2	0	1	0	1	01	1	01
Anopheles	0	0	1	1	0	1	2	1	1	0	1	2	1	0	0	0	0	0	0	1	12	0	0	1	1
Armigeres	0	0	1	1	1	0	0	2	0	0	1	1	1	12	1	1	0	2	0	1	0	1	1	01	0
Bironella	0	0	1	1	0	1	2	1	1	0	1	2	1	0	0	0	01	0	0	1	2	0	0	1	1
Chagasia	1	1	1	1	0	0	2	1	1	0	1	2	1	0	0	0	0	0	0	1	1	0	0	1	1
Coquillettidia	1	1	1	1	1	1	1	2	0	0	0	2	0	1	1	1	0	1	0	1	0	1	0	1	1
Culex	0	1	1	1	1	0	0	2	1	0	1	2	0	123	1	1	0	2	0	1	0	1	01	1	01
Culiseta	0	0	1	1	1	0	0	2	1	1	1	2	0	1	1	1	0	1	0	1	0	1	0	1	1
Deinocerites	0	1	1	1	1	0	0	2	0	0	1	2	0	1	1	1	1	2	2	1	0	1	0	1	0
Eretmapodites	0	0	2	1	1	0	0	2	0	0	1	2	1	1	1	1	0	2	0	1	0	1	0	1	0
Ficalbia	0	1	1	1	1	0	0	2	1	0	1	1	0	2	1	1	0	2	2	1	0	1	0	1	1
Galindomyia	0	1	1	1	1	0	0	2	1	0	1	1	0	2	1	1	1	2	2	1	0	1	1	1	0
Haemagogus	0	1	2	1	1	0	0	2	0	0	1	1	1	1	1	1	0	2	2	1	0	1	1	0	0
Heizmannia	0	1	1	1	1	0	0	2	0	0	1	1	1	23	1	1	0	2	2	1	0	1	1	01	0
Hodgesia	1	0	1	1	1	0	0	2	1	0	1	0	0	1	1	1	1	3	3	1	0	1	1	1	0
Isostomyia	0	0	2	0	1	0	0	2	0	0	0	1	0	3	1	1	0	3	3	1	0	2	1	1	0
Johnbelkinia	0	0	2	0	1	0	0	2	0	0	0	1	0	3	1	1	0	3	0	1	0	2	1	1	0
Limatus	0	0	2	0	1	0	0	2	0	0	0	1	0	3	1	0	1	3	3	1	0	2	1	0	0
Malaya	0	0	2	0	1	0	0	2	0	0	0	0	1	3	1	0	1	3	3	1	0	2	1	0	0
Mansonia	1	1	1	01	1	0	1	2	0	0	0	2	0	1	1	1	0	2	0	1	0	1	0	1	1
Maorigoeldia	0	0	2	1	1	0	0	2	0	0	0	1	0	3	1	1	0	2	2	1	0	1	1	1	1
Mimomyia	1	1	1	1	1	0	0	2	01	0	01	12	01	12	1	1	0	2	1	1	0	1	1	1	1
Opifex	0	0	1	1	1	0	0	2	0	0	1	0	1	1	0	1	1	2	2	1	0	1	0	1	1
Onirion	0	0	2	0	1	0	0	2	0	0	0	1	0	3	1	1	0	3	3	1	0	2	1	1	0
Orthopodomyia	0	0	1	1	1	0	0	2	0	0	1	2	1	1	1	1	0	1	0	1	0	1	0	1	1
Phoniomyia	0	0	2	0	1	0	0	2	0	0	0	0	0	3	1	1	1	3	3	1	0	2	1	1	0
Psorophora	0	0	1	1	1	0	0	2	0	0	1	2	0	1	1	1	0	2	0	1	0	1	0	1	1
Runchomyia	0	0	2	0	1	0	0	2	0	0	0	1	0	3	1	1	1	3	3	1	0	2	1	1	0
Sabethes	0	0	2	0	1	0	0	2	0	0	0	1	0	3	1	1	1	3	3	1	0	2	1	0	0
Shannoniana	0	0	2	0	1	0	0	2	0	0	0	1	0	3	1	1	0	3	0	1	0	2	1	1	0
Topomyia	0	0	2	01	1	0	0	2	0	0	0	0	0	3	1	1	1	3	3	1	0	1	1	1	0
Toxorhynchites	0	0	2	0	1	0	2	01	1	1	0	1	0	2	1	1	0	1	0	1	2	0	1	1	0
Trichoprosopon	0	0	2	0	1	0	0	2	0	0	0	1	0	3	1	1	0	3	0	1	0	2	1	1	0
Tripteroides	0	0	2	1	1	0	0	2	0	0	0	1	0	3	1	1	0	3	3	1	0	2	1	1	0
Udaya	0	0	1	1	1	0	0	2	0	0	1	1	1	2	1	1	0	2	0	1	0	1	1	1	0
Uranotaenia	0	1	1	1	1	0	2	2	1	0	1	2	0	2	1	1	0	4	4	1	0	1	0	1	1
Wyeomyia	0	0	2	0	1	0	0	2	0	0	0	01	0	3	1	1	1	3	3	1	0	2	1	0	0
Zeugnomyia	0	1	2	1	1	0	0	2	0	0	1	1	1	1	1	1	0	2	3	1	0	1	1	1	0

Appendix 2, continued.

	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	6	7	7	7	7
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3
Corethrella	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0
Eucorethra	1	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	1	1	0
Mochlonyx	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0
Nothodixa	1	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	1	0	1	0	0	0
Aedeomyia	1	1	0	1	1	0	0	1	1	1	0	1	1	0	1	0	1	1	1	0	0	0	0
Aedes	1	1	0	01	1	0	1	1	1	01	0	1	1	0	1	0	1	1	0	0	0	01	1
Anopheles	1	0	0	0	0	1	0	1	1	0	0	1	0	1	1	1	1	1	0	0	0	0	0
Armigeres	0	1	0	1	1	0	01	1	1	01	0	1	1	0	1	0	1	1	0	1	0	1	1
Bironella	1	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	1	0	0	0	0	0
Chagasia	1	1	0	1	1	1	0	1	1	0	0	1	0	1	1	0	1	1	0	0	0	0	0
Coquillettidia	1	1	0	0	1	0	01	1	1	1	0	1	1	0	1	0	1	1	0	0	0	1	1
Culex	1	1	0	0	1	0	0	1	1	1	0	1	1	0	1	0	1	1	0	0	1	1	2
Culiseta	1	1	0	1	1	1	0	1	1	1	0	1	1	0	1	0	1	1	0	0	0	1	1
Deinocerites	1	1	1	0	1	0	0	1	1	1	0	1	1	0	1	0	1	1	0	0	1	1	2
Eretmapodites	1	1	1	0	1	0	1	1	0	0	0	1	1	0	1	0	1	1	0	0	0	1	1
Ficalbia	1	1	0	0	1	0	0	1	1	0	0	1	1	0	1	0	1	1	0	0	0	0	1
Galindomyia	1	1	1	0	1	0	0	1	1	1	0	1	1	0	1	0	1	1	0	0	1	1	2
Haemagogus	0	1	01	1	1	0	1	1	0	0	0	1	1	0	1	0	1	1	0	0	0	1	1
Heizmannia	0	1	01	1	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	1	0	1	1
Hodgesia	1	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1
Isostomyia	0	1	1	0	0	1	0	1	0	0	0	1	1	0	1	0	1	1	0	1	0	1	1
Johnbelkinia	0	1	1	0	1	1	0	1	0	0	0	1	1	1	1	0	1	1	0	1	0	1	1
Limatus	0	1	1	0	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0	1	0	1	1
Malaya	0	1	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0	1	0	1	0	1	1
Mansonia	1	1	0	0	1	0	1	1	1	1	0	1	1	0	1	0	1	1	0	0	0	1	1
Maorigoeldia	1	1	0	0	1	1	0	1	1	0	0	1	1	1	1	0	1	1	0	0	0	1	1
Mimomyia	1	1	0	0	1	0	0	1	1	0	0	1	01	0	0	0	1	1	0	0	0	01	1
Opifex	1	1	0	0	1	0	1	1	1	1	0	1	1	0	1	0	1	1	0	0	0	1	1
Onirion	0	1	1	0	0	1	0	1	0	0	0	1	1	0	1	0	1	1	0	1	0	1	1
Orthopodomyia	1	1	0	0	1	0	0	1	1	0	0	1	1	0	1	0	1	1	1	0	0	1	1
Phoniomyia	0	1	1	0	0	1	0	1	0	0	0	0	1	0	1	0	1	1	0	1	0	1	1
Psorophora	1	1	0	0	1	1	1	1	1	1	0	1	1	0	1	0	1	1	0	0	0	1	1
Runchomyia	0	1	1	0	1	1	0	1	0	0	0	1	1	01	1	0	1	1	0	1	0	1	1
Sabethes	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	1	0	1	1
Shannoniana	0	1	1	0	0	1	0	1	0	0	0	1	1	1	1	0	1	1	0	1	0	1	1
Topomyia	0	1	0	0	1	1	0	1	0	0	1	0	1	0	1	0	1	1	0	1	0	01	1
Toxorhynchites	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	1	1	1	0	1	0	1	1
Trichoprosopon	0	1	1	0	1	1	0	1	0	0	0	1	1	1	1	0	1	1	0	1	0	1	1
Tripteroides	01	1	01	0	1	1	0	1	0	0	01	1	1	0	1	0	1	1	0	1	0	01	1
Udaya	0	1	0	1	1	0	1	1	1	0	0	0	1	0	1	0	1	1	0	1	0	1	1
Uranotaenia	1	1	0	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Wyeomyia	0	1	1	0	0	1	0	1	0	0	0	01	1	01	1	0	1	1	0	1	0	01	1
Zeugnomyia	0	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	1	0	1	1

APPENDIX 3

Character state changes of relevant characters on the branches of the cladogram (Fig. 1B) obtained when the constant of concavity, *K*, in PIWE is set to 1. Changes are not listed for Culicini and terminal taxa.

Node 58
ch. 8: 0 → 2
Node 59
ch. 8: 0 → 1
Node 60
ch. 64: 0 → 1
Node 61
ch. 6: 0 → 1
Node 62
ch. 49: 1 → 0
Node 63
ch. 2: 0 → 1
ch. 42: 0 → 1
ch. 62: 1 →
Node 64
ch. 2: 0 → 1
ch. 37: 1 → 0
ch. 42: 0 → 1
ch. 61: 0 → 1
ch. 62: 1 → 0
Node 66
ch. 55: 1 → 0
Node 67
ch. 53: 0 → 1
Node 68
ch. 29: 1 → 0
Node 69
ch. 43: 2 → 3
ch. 44: 2 → 3
ch. 47: 1 → 2
ch. 59: 1 → 0
ch. 70: 0 → 1
Node 70
ch. 7: 0 → 1
ch. 10: 2 → 1
ch. 15: 1 → 0
ch. 16: 0 → 1
ch. 24: 4 → 1
ch. 27: 1 → 0
ch. 28: 1 → 2
ch. 36: 1 → 2
ch. 39: 1 → 3
ch. 56: 0 → 1

CONSPECTUS OF TAXONOMIC CHANGES

New Taxa

aenigma, sp.n.
celatum, sp.n.
imparis, sp.n.
Onirion, gen.n.
regale, sp.n.

Changes in Taxonomic Status

Wyeomyia brucei, to specific rank, from *Wyeomyia* to *Onirion*
Wyeomyia belkini, synonymy with *brucei*
Goeldia luederwaldti, synonymy with *personatum*
Wyeomyia sirivanakarni, from *Wyeomyia* to *Onirion*
Dendromyia personata, from *Wyeomyia* to *Onirion*

TAXONOMIC INDEX

Synonyms are in *italics*; main citations are in **bold**.